SURVEY OF FLOWER VISITING BY ACULEATE WASPS AND BEES IN THE SEMI-ARID TO ARID AREAS OF SOUTHERN AFRICA

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ABSTRACT

The results of a survey of flowers visited by aculeate wasps and bees in the semi-arid to arid areas of southern Africa, i.e. the Karoo Biome and associated dry fynbos, arid savanna and desert fringes, are presented. Flowers of 36 plant families, represented by c 600 species, were recorded as visited by aculeate wasps and bees. Visitation of flowers by family is examined and discussed, based on 16,229 records for visits by 927 species of solitary aculeate wasps and bees: 129 species of masarine wasps (pollen wasps); 375 species of non-masarine wasps; and 423 species of bees. Differences in assemblages of visitors between families, within families between sub-families, tribes, genera and species and across geographic gradients are noted. The dependability or lack of dependability of visitors based on the degree of polyphagy or oligophagy exhibited is discussed. The potential of visitors as pollinators is suggested where sufficient records and observations on flower fit and visitor behaviour are available.

Keywords: Karoo Biome, Kalahari, Namib desert, dry fynbos, dry savannah, pollination, pollinators, polyphagy, oligophagy, monophagy, Hymenoptera, behaviour, taxonomic surveys

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INTRODUCTION

The present contribution is a first attempt at a comparative overview of flower visiting by aculeate wasps and bees in the semi-arid to arid areas of southern Africa, i.e. the Karoo Biome and associated dry fynbos, arid savanna and desert fringes. It follows two previous publications based on work done in the same area and sourced from the same database: Gess & Gess (2004a) deals with the distributions of flower associations of pollen wasps (Vespidae: Masarinae) and Gess & Gess (2004b) is a comparative overview of flower visiting by non-*Apis* bees. The paper on flower visiting by bees, can be regarded as the reverse of the present paper, that is it presents and discusses flower visiting by bee taxa whereas the present paper presents plant taxa and discusses which aculeate wasps and bees visit them.

Flowers of 36 plant families, represented by c. 600 species (c. 400 identified to species and the remainder only to genus or family), were recorded as visited by aculeate wasps and bees to obtain floral resources Visitation of flowers by family is examined and discussed, based on a catalogue of 16,229 records (supported by voucher specimens) for visits by 927 species of solitary aculeate wasps and bees (Gess & Gess 2003). Differences in assemblages of visitors – between families, within families between sub-families, tribes, genera and species and across geographic gradients, from south to north and west to east – are noted. The dependability or lack of dependability of visitors – based on the degree of polyphagy or oligophagy exhibited – is discussed. The potential of visitors as pollinators is suggested where sufficient records and observations on flower fit and visitor behaviour are available.

The records are supported by voucher specimens. For further details on the database associated with these records, see page 3 (under 'Database').

The majority of specimens, those collected by the authors, are linked by note numbers which further link them to fieldnotes. The published catalogue (Gess & Gess 2003) gives approximate localities; however, exact localities, in most cases with co–ordinates, are recorded on the specimen labels and, in the case of the bees, in an electronic relational database held at the Albany Museum, Grahamstown, by the African Pollinator Initiative (API) and the South African Biodiversity Information Facility (SABIF). The sexes of the insect specimens are given in the catalogue and bee database, however.

When collecting specimens, distinction between pollen and nectar collection was not always made and thus, except where specifically referred to, the present discussion encompasses both types of visits indiscriminately. Those species visiting flowers of taxonomically–divers plants are termed polyphagous (*sensu* Struck 1994). Degrees of polyphagy from narrow to broad are recognized. The term oligophagous is limited in the present paper to species visiting flowers of plants belonging to a single family, subfamily, tribe or genus. Few monophagous species, i.e. those restricted to single species of plant, were encountered.

In order to facilitate ease of reading, in the present paper all solitary aculeate wasps that visit flowers for adult nourishment only are referred to simply as wasps. The pollen wasps (Vespidae: Masarinae), like the majority of bees, visit flowers not only for adult nourishment but also to gather pollen and nectar for provisioning their nest cells.

The bees included in the analysis are all bee taxa, excluding the social Apinae. Honeybees, *Apis mellifera*, and meliponines taken in samples are referred to in the text.

It has been stated, erroneously, that in the Aculeata long proboscises are found only among the bees (Kevan & Baker 1983). Although it is true that a short proboscis is characteristic of the majority of wasps, elongation of the proboscis has taken place in several wasp taxa, for example, *Bembix* (Nyssonidae), *Ammophila* (Sphecidae) and *Raphiglossa* (Vespidae: Eumeninae). In the majority of pollen wasps the glossa is markedly elongated. In many species of *Quartinia* the glossa is considerably longer than the wasp's body length from the frons to the tip of the abdomen.

Consequently, pollen wasps have the potential to obtain nectar from a wide range of flower forms including many in which the nectar is not readily accessible.

METHODS

STUDY AREA

The study area is constituted of the Karoo Biome of Rutherford (1997) together with the Fynbos fringe in the southwest and the Desert and Savanna fringes in the north (Figure 1).

The vegetation of the entire area is characterized by low scrub with taller shrubs and/or trees mainly restricted to drainage channels and hill slopes (Plates 1 – 16). The scrub vegetation varies according to regional rainfall, from sparse (over most of the area, which receives from 100-500 mm precipitation per annum) to extremely sparse (along the fringes of the Namib which receives less than 100 mm precipitation per annum). Succulence is particularly associated with the winter rainfall region, resulting in this part of the Karoo Biome being termed the Succulent Karoo Biome (Rutherford & Westfall 1986). The summer rainfall region of the Karoo – with a lower level of succulence and a higher grassy element – is known as the Nama Karoo Biome (Rutherford & Westfall 1986).

Detailed reviews of the climate, topography, geology and vegetation of the study area are presented by various authors in Cowling *et al.* (1997) and Dean & Milton (1999).

The aculeate wasp and bee fauna of the southern Karoo is polarized into two main faunal groups, one centered in the west and the other in the east. Between the two extremes lies a transition of overlapping subtraction margins of the eastern and western faunas corresponding with the interface between the winter rainfall and summer rainfall regions (Gess & Gess 1993). To the north there are strong affinities with the arid savanna fauna. Sampling in the Namib Desert was principally in the drainage channels

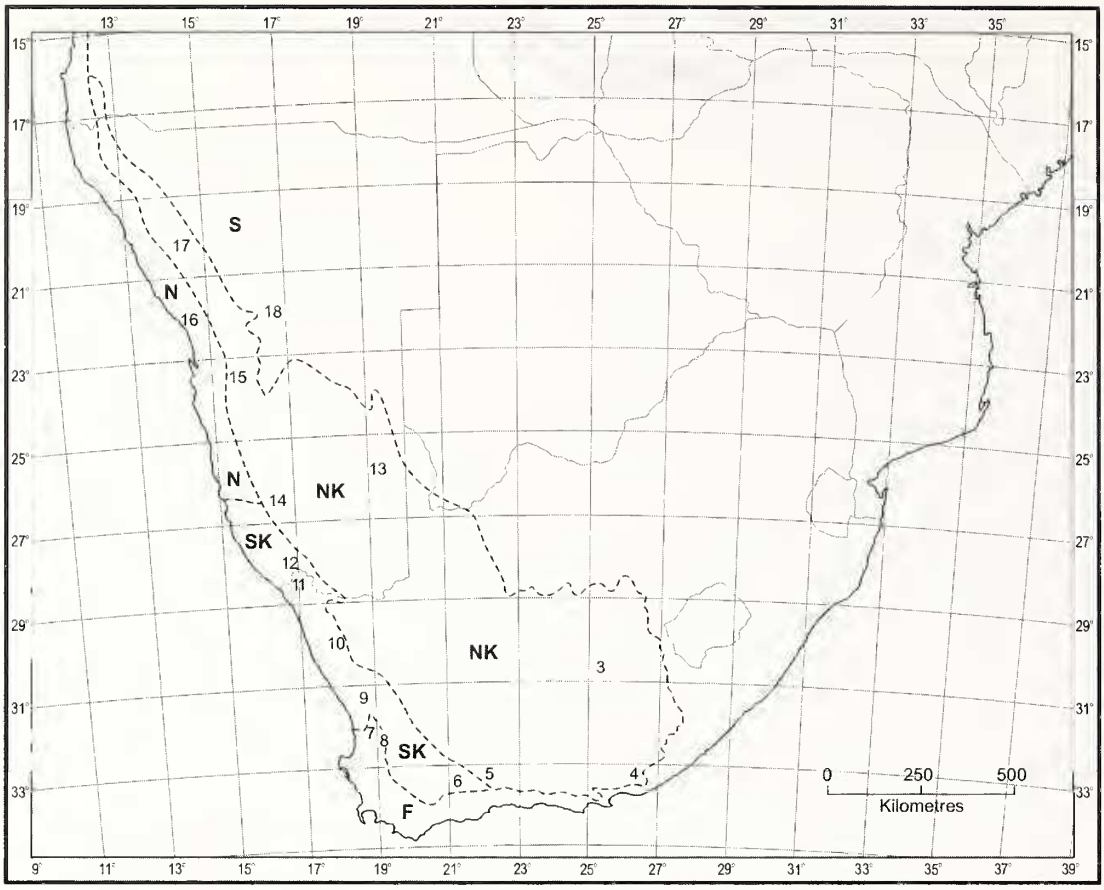

Fig. 1. Southern Africa. Distributions of Fynbos (F), Succulent Karoo (SK), Nama Karoo (NK), Desert (Namib) (N) and Savanna (S) biomes, after Rutherford (1997). Digits 3 - 18 denote areas illustrated in figures 3 – 18.

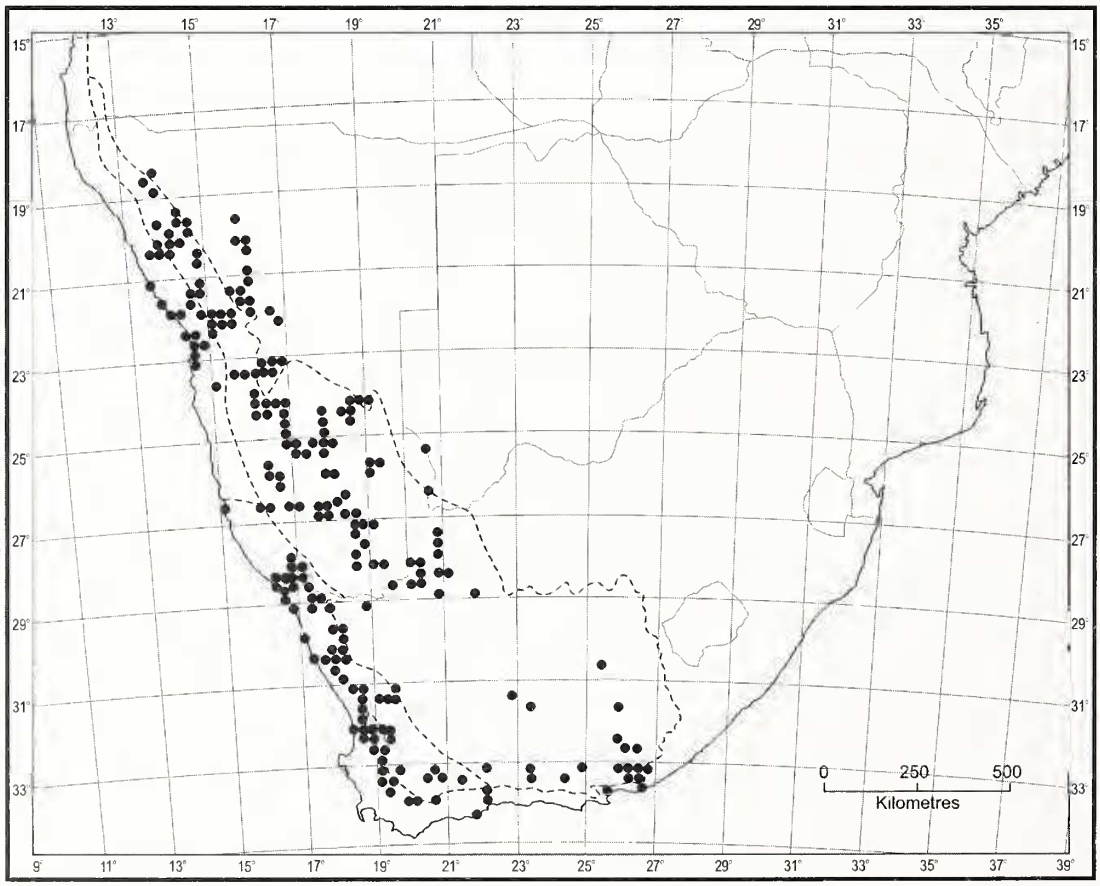

Fig. 2. Distribution of flower visitor sampling sites.

where there is a recognizable desert faunal element, with penetration by savanna species from the east and coastal species from the west. Pollen wasps show their highest species diversity in southern Africa and in particular in the west, species diversity falling off markedly from west to east (Gess 1992a, 1996).

SAMPLING SITES AND TIMES

The distribution of the sampling sites within the semi-arid to arid areas of southern Africa is shown in Figure 2.

Each dot covers a quarter degree square in which is included one or more sampling sites. Sampling to the east and south has taken place during the past thirty years, principally from 1972 to 1985; that in the west north of the Olifants River Mountains to the southern Richtersveld principally from 1985 to 1996; that in northern Richtersveld principally from 1996 to 1998; and that in Namibia principally from 1997 to 2000.

Apart from the area in which the authors are resident (Grahamstown, Eastern Cape) it has not been possible to sample throughout the year. Seasonal timing of sampling by the authors has been based on experience and the general rainfall and temperature patterns of different areas. The distribution and magnitude of rainfall events, and therefore of flower patches in the semi–arid and arid areas of southern Africa, is unpredictable. Thus, although general sampling areas and sampling times have been purposefully selected, the choice of sampling sites has of necessity been opportunistic.

In the southeast and south the peaks of rainfall are in September and March and the summer is rarely excessively hot and dry. Thus sampling has been principally from late October through to March. In the winter rainfall region of the southwest, north to Lüderitz and Aus, sampling has been from August, when temperatures start to rise, through to December, when most flowering is over and the land as a general rule becomes parched. North of the Orange River in the southern Kalahari, southeastern Namibia and in western Namibia to the north of the winter rainfall area, sampling has been in March and April, which is when rains are expected and the excessive heat of summer is over.

SAMPLING METHODS

Solitary aculeate wasps and bees visiting flowers were collected using a hand net. All plants in flower at the study sites were observed for visitors and, when possible, were sampled over periods throughout the day. In effect, wasps and bees in an area were all being offered the choice of visiting all those plants in flower. Each site sampled therefore represented a 'choice chamber', in which all the wasps and bees were offered the same choice of plants in flower.

DATABASE

The database used for the analysis is *A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa* (Gess & Gess 2003). It is constituted of 16,229 records of visits to c 600 species of plants by solitary aculeate wasps and bees, 927 species in all. Of these records, 98.2% were derived from deliberate sampling by the authors (assisted at various times and sites by D.W. Gess, H.W. Gess and R.W. Gess). The remaining records have been assembled from label data from the Albany Museum collection, mostly concurrently collected material from the eastern karroid areas (C.F. Jacot Guillarmod, 219 records; J.G.H.Londt, 66 records; A.J.S Weaving, 30 records). Published records by other authors are taken into account in the discussion but have not been included in the database for analysis.

The records are supported by voucher specimens. The majority of specimens – those collected by the authors – are linked by note numbers that further link them to fieldnotes. The catalogue gives approximate localities. However, exact localities – in most cases with co-ordinates – are recorded on the specimen labels, and in the case of the bees in an electronic relational database initiated by the authors and held at the Albany Museum, Grahamstown, by the African Pollinator Initiative (API) and the South African Biodiversity Information Facility (SABIF). The sexes of the insect specimens are given in the catalogue and bee database.

The great majority of the insect specimens are housed in the terrestrial insect collection of the Albany Museum, Grahamstown. Specimens of many, but not all, of the plants have been deposited in the Sehönland Herbarium, Albany Museum. Duplicates of specimens from Namibia are in the National Herbarium of Namibia, Windhoek.

IDENTIFICATIONS

The majority of specimens of both insects and plants were identified to species and the remainder to genus or family.

The great majority of the specimens of wasps and bees were identified by the second author. Other hymenopterists who were undertaking generic revisions were responsible for some of the identifications as follows:

- Alexander Antropov, Moscow Lomonosov State University, Russia – *Gessus* Antropov (Crabronidae: Crabroninae);
- Connal Eardley, PPRI, ARC Pretoria – Anthophorini and Eucerini (Apidae: Apinae) prior to 1985, Ammobatini (Apidae: Nomadinae) prior to 1991, *Lithurgus* Berthold (Megachilidae: Megachilinae) prior to 1987, and *Scrapter* Lepeletier (Colletidae) prior to 1991;
- Michael Kuhlmann, University of Munster, Germany – *Colletes* Latreille (Colletidae);
- Wojciech Pulawski, California Academy of Sciences – *Tachysphex* Kohl (Crabronidae: Larrinae).

The identifications of the specimens of plants were undertaken by the following botanists: Grace Britten and Estelle Brink, Herbarium, Albany Museum (various groups); Coleen Mannheimer, National Herbarium, Windhoek (the majority of the plants from Namibia); Sabene Austhaller and Patricia Craven, National Herbarium, Windhoek (some plants from Namibia); Jo Beyers, then of Stellenbosch Herbarium (especially *Wahlenbergia* and *Microcodon*); Jan Vlok, then of Saarsveld Forestry Centre, George (*Aspalathus spinescens* Thunberg); Sue Dean, then

Table 1. Numbers and percentages of species of wasps, pollen wasps and bees recorded visiting flowers of the listed plant families, together with the Index of Diversity of Choice[1] at the specific level for each major group (wasps, pollen wasps and bees). Asterisks draw attention to the six families attracting the highest number of species.

Plant taxa	Wasps (375 spp) no.	%	Pollen Wasps (129 spp.) no.	%	Bees (423 spp.) no.	%	Totals w+pw+b (927 spp.) no.	Percentage w+pw+b %
MONOCOTS								
Asparagales								
Asparagaceae	10	2.67					10	1.08
Asphodelaceae			1	0.78	12	2.84	13	1.40
Iridaceae			2	1.55	12	2.84	14	1.51
EUDICOTS								
Proteaceae	15	4.00			8	1.89	23	2.48
CORE EUDICOTS								
Caryophyllales								
Aizoaceae*	76	20.27	60	46.51	98	23.17	234	25.24
Amaranthaceae	42	11.20	1	0.78	24	5.67	67	7.23
Molluginaceae	46	12.27	5	3.88	19	4.49	70	7.35
Nyctaginaceae	2	0.53	2	1.55	3	0.71	7	0.76
Plumbaginaceae	3	0.08	3	2.33	2	0.47	8	0.83
Portulacaeae	3	0.08					3	0.32
Saxifragales								
Crassulaceae			2	1.55	7	1.65	9	0.97
ROSIDS								
Zygophyllaceae*	51	13.6	17	13.18	71	16.78	139	14.99
Geraniales								
Geraniaceae	5	1.33	8	6.20	6	1.42	19	2.05
EUROSIDS I								
Celastraceae	40	10.67			7	1.65	47	5.06
Cucurbitales								
Cucurbitaceae					7	1.65	7	0.76
Fabales								
Fabaceae*	147	39.2	11	8.53	164	38.77	322	34.74
Polygalaceae					9	2.13	9	0.97
Malpighiales								
Euphorbiaceae	15	4.0	1	0.78	3	0.71	19	2.05
Rosales								
Rhamnaceae	35	9.33			1	0.24	36	3.88
EUROSIDS II								
Brassicales								
Brassicaeae	2	0.53	3	2.33	32	7.57	37	3.99
Malvales								
Malvaceae	5	1.33	8	6.20	54	12.77	67	7.23
Neuradaceae	1	0.27	1	0.78	10	2.36	12	1.29
Sapindales								
Rutaceae	1	0.27			1	0.24	2	0.22
ASTERIDS								
Cornales								
Loasaceae					2	0.47	2	0.22
EUASTERIDS I								
Boraginaceae	13	3.47	5	3.88	50	11.82	68	7.34
Vahliaceae	1	0.27	1	0.78	7	1.65	9	0.97
Gentianales								
Apocynaceae	48	12.80			31	7.33	79	8.52
Lamiales								
Acanthaceae	14	3.73	2	1.55	52	12.29	68	7.34
Lamiaceae	10	2.67	2	1.55	65	15.37	77	8.31
Pedaliaceae					9	2.13	9	0.97
Scrophulariaceae*	27	7.20	33	25.58	38	8.98	98	10.57
Solanales								
Convolvulaceae					1	0.24	1	0.08
Solanaceae	8	2.13			11	2.60	19	2.05
EUASTERIDS II								
Apiales								
Apiaceae*	161	42.93			27	6.38	188	20.28
Asterales								
Asteraceae*	116	30.93	56	43.41	157	37.12	329	35.49
Campanulaceae	9	2.40	19	14.73	33	7.80	61	6.58
Index of Diversity of Choice	141.60		88.37		144.21			

[1]See page 9 for definition of Index of Diversity of Choice

Table 2. Numbers of speeies of bees, by family, reeorded visiting flowers of the listed plant families together with the Index of Diversity of Choice[1] at the speeifie level for eaeh bee family.

Plant taxa	Andrenidae (9 spp.)	Apidae (123 spp.)	Colletidae (46 spp.)	Halictidae (69 spp.)	Megachilidae (146 spp.)	Melittidae (30 spp.)
MONOCOTS						
Asparagales						
Asparagaceae						
Asphodelaceae		2	1	1	8	
Iridaceae		3	1	4	2	2
EUDICOTS						
Proteaceae		3	3	1		1
CORE EUDICOTS						
Caryophyllales						
Aizoaceae	4	35	10	21	21	7
Amaranthaceae		5	3	10	5	1
Molluginaceae	4	7		4	2	2
Nyctaginaceae	1			1	1	
Plumbaginaceae		1		1		
Portulacaeae						
Saxifragales						
Crassulaceae		2		2	2	1
ROSIDS						
Zygophyllaceae	3	22	10	23	10	3
Geraniales						
Geraniaceae		3	1		2	
EUROSIDS I						
Celastraceae		1	1	5		
Cucurbitales						
Cucurbitaceae		4		1	1	1
Fabales						
Fabaceae	6	41	3	22	80	12
Polygalaceae		2			7	
Malpighiales						
Euphorbiaceae			1	2		
Rosales						
Rhamnaceae				1		
EUROSIDS II						
Brassicales						
Brassicaeae		17	1	6	7	1
Malvales						
Malvaceae	1	21		10	19	3
Neuradaceae		2	1	2	4	1
Sapindales						
Rutaceae				1		
ASTERIDS						
Cornales						
Loasaceae				1	1	
EUASTERIDS I						
Boraginaceae	2	29		6	13	
Vahliaceae		4		1	2	
Gentianales						
Apocynaceae		9	1	5	15	1
Lamiales						
Acanthaceae		28		4	20	
Lamiaceae	2	31		7	25	
Pedaliaceae		4		2	3	
Scrophulariaceae	1	12	4	15	4	2
Solanales						
Convolvulaceae		1				
Solanaceae		8		3		
EUASTERIDS II						
Apiales						
Apiaceae		8	6	9	4	
Asterales						
Asteraceae	1	51	19	29	53	4
Campanulaceae		8	3	7	7	8
Index of Diversity of Choice	177.77	195.93	50.00	202.90	117.81	70.00

[1]See page 9 for definition of Index of Diversity of Choiee

of the Karoo Biome Research Station (some mesems), and the first author (various).

For ease of reading, generic and specific names are given without authors in the text but are listed with authors in the indexes to insects and plants at the end of this publication.

CLASSIFICATION SYSTEMS

The classification of flowering plants follows that of 'The Angiosperm Phylogeny Group' (APG 1998). This is based on recent cladistic analyses, which have established many of the elements of the major branching sequence of flowering plant phylogeny. Most of the families have been grouped into putatively monophyletic orders and monophyletic, informal, higher groups. Under these informal groups (monocots, commelinoids, eudicots, core eudicots, rosids including eurosids I and II, and asterids including euasterids I and II) are also listed some of the families not assigned to any order. At the end of the system are placed the remainder of the families, for which no firm data existed regarding their placement in the system. A simplified cladogram – based principally on that presented in APG (1998), but including only families recorded from southern Africa – is presented in Leistner (2000). The classification in Tables 1 and 2 are further simplified to include only those families that received visits from wasps, pollen wasps or bees during the present survey.

Following Hartmann (1991), Aizoaceae with petaloid staminodes – in fact those plants commonly termed 'mesems' and previously classified as Mesembryanthemaceae – are referred to by the collective term Mesembryanthema. Those Aizoaceae not included in this informal group are referred to as Aizoaceae: non-Mesembryanthema.

The classification of wasps and bees at superfamily level and of wasps at family level follows that used by Goulet & Huber (1993), and that of Michener (2000) for bees below superfamily level. (Appendix 1).

GLOSSARY

Aculeates: an acceptable word used to mean Aculeate Hymenoptera. In the present context it should be understood to be a collective term for aculeate wasps and bees only, as ants were not included in the survey.

Cyathium: in Euphorbiaceae, a subunit of a cymose inflorescence, that is flower-like in appearance. It is composed of a female and several male flowers, lacking petals and sepals, which are united within a cup-like structure surrounded by bacts that are colouorful in most species.

Flower visiting

Casual visitors: visitors that are commonly associated with flowers of other taxa but are very occasionally found on the flowers under consideration.

Dependable visitors: visitors that are oligophagous and can therefore be depended upon to visit flowers of cetain taxa even when other taxa in flower may be more abundant.

Expected visitors: visitors that, based on the nature of the flowers visited or the frequency of their association with the flowers under consideration, can be expected to be visitors of those flowers.

Legitimate visitors: flower visitors that, in terms of their size and behaviour, have the potential to pollinate the flowers being visited.

Thieves: visitors that are able to and do remove nectar and/or pollen without pollinating the flowers. These visitors are said to steal the nectar and/or pollen.

Trip (tripping): in papilionate 'pea flowers', the stamens and gynoecium are enclosed by the two lower petals in what is termed the keel. A visitor of a suitable weight and size landing on the wing petals to the sides of the keel or the standard petal at the "top" of the flower, when reaching for the nectar enclosed in the basal part of the flower, causes the keel petals to open and the stamens and style to protrude. This is called 'tripping' the flower. Some visitors, such as honeybees, *Apis mellifera*, reach the nectar from the side of the base of the flower and do not trip the flower. Thus, they 'steal' the nectar.

–phagous

Polyphagous: visiting flowers of a wide range of families.
Broadly polyphagous: visiting flowers of a large number of families.
Narrowly polyphagous: visiting flowers of a small number of families.
Oligophagous: visiting a limited range of flowers of species of plants all belonging to one family or genus.
Monophagous: visiting flowers of one species of plant.

Pollinium: a mass of cohering pollen grains, produced by such plants as asclepiads and orchids, transported as a whole during pollination.

RESULTS AND SYNTHESIS

DIVERSITY OF PLANT TAXA VISITED

Flowers of 36 families of flowering plants were recorded as receiving visits from aculeate wasps and bees. Of the 36 plant families, 34 received visits from bees, 29 from wasps and 21 from pollen wasps (Table 1).

Visits were by 927 species of wasps, pollen wasps and bees (375 species of wasps, 129 species of pollen wasps and 423 species of bees). The two families not receiving visits from bees – which, however, received visits from wasps – were Asparagaceae (previously included in Liliaceae) and Portulacaceae.

Cowling & Hilton-Taylor (1999, Table 4.1) list the 10 largest plant families from each of five domains (Namaqualand-Namib semi-arid, Namaqualand-Namib arid, Southern Karoo, Eastern Karoo and Damaraland-Kaokoveld) of the Karoo-Namib Region (15 families in all) namely Asteraceae, Aizoaceae, Acanthaceae, Asclepiadaceae (included in Apocynaceae in APG 1998), Chenopodeaceae, Capparaceae, Crassulaceae, Euphorbiaceae, Fabaceae, Geraniaceae, Scrophulariaceae, Sterculiaceae (included in Malvaceae in APG 1998), Iridaceae, Liliaceae and Poaceae. The 36 families recorded in the present survey as visited by solitary aculeate wasps and bees include all the above-listed families except Poaceae and Chenopodiaceae.

When considering the 10 families receiving visits from the highest numbers of species of wasps, pollen wasps and bees (Table 1), one finds six of the Cowling and Hilton–Taylor families included, namely Asteraceae (visited by 329 species), Fabaceae (visited by 322 species), Aizoaceae (visited by 234 species), Scrophulariaceae (visited by 98 species), Asclepiadaceae (included in Apocynaceae) (visited by 79 species), and Acanthaceae (visited by 68 species). The remaining four families were Apiaceae (visited by 188 species), Zygophyllaceae (visited by139 species), Lamiaceae (visited by 77 species) and Boraginaceae (visited by 68 species). Although these are not amongst the10 largest plant families, they are nonetheless amongst the families that characterise the Karoo–Namib Region.

Specific flower visitors show varying degrees of diversity of choice, i.e. of oligophagy and polyphagy. In order to make comparisons between groups of flower visitors constituted of unequal numbers of species Gess (1992b, unpublished) developed an Index of Diversity of Choice at the specific level, using the formula:

$D = a\text{-}b/b \times 100$

where a = the sum of the number of species recorded visiting each of the flower families and b = the number of species of flower visitors (published in Gess 1996 page 47). This is an index by which to compare the degree of oligophagy or polyphagy exhibited by taxa of differing numbers of species. 'D' would equal 0 if each species only visited one species of plant; the higher the value of 'D' the greater the degree of polyphagy.

When this formula is applied to the database (Gess & Gess 2003) as summarized in Table 1 the following values of D are obtained: wasps 141.60; pollen wasps 88.37; and bees 144.21. These values indicate a markedly narrower diversity of choice of flowers by pollen wasps overall than by wasps or bees.

Marked variations in diversity of flower visiting between families of bees are apparent (Table 2 and Gess & Gess 2004b). The following 'D' values were calculated for individual bee families: Andrenidae 177.77; Colletidae 50.00; Halictidae 200.00; Melittidae 66.67; Megachilidae 117.81; Apidae (excluding *Apis mellifera*) 195.93. These values indicate a similarly low diversity of choice for Colletidae and Melittidae and a greater diversity of choice for Megachilidae, Andrenidae, Apidae and Halictidae, in that order. The low diversity of choice for Colletidae and Melittidae is comparable with that (88.37) obtained for pollen wasps.

With the exception of Colletidae, the present values are higher than those obtained in an earlier analysis (Gess 1992b), even if recalculated using the presently–used classifications. Taking into account that the 1992 database excluded the Richtersveld National Park and the southern and western arid areas of Namibia, this could be indicative of a number of possible factors: an overall higher degree of polyphagy; a higher degree of opportunistic foraging to the north, where rainfall is more unpredictable; a shift in plant families visited along ecological gradients in the case of widely-distributed species; or a combination of these factors (Gess & Gess 2004a).

PLANT FAMILIES AND THEIR VISITORS

MONOCOTS

In the study areas, at the times of year when sampling took place, relatively few monocots attracting solitary aculeate wasps and bees were encountered. Indeed, many of the showy species forming spectacular expanses, which are a feature of marshy ground and 'rock gardens' in spring and early summer in the southwest, are not patronized by aculeate wasps and solitary bees but by flies and beetles (Goldblatt & Manning 2000a, 2000b; Goldblatt *et al.* 1995, 2002; Manning & Goldblatt 2001).

Despite the small number of monocot species sampled in the present survey, visits were recorded for all bee families except Andrenidae, which are, however, known to visit some *Gladiolus* (Goldblatt *et al.* 1998a, 1998 b). No species restricted to monocots were found.

Goldblatt and his co–workers have established that solitary bees contribute to the pollination of some Iridaceae, species of *Moraea* (Goldblatt & Bernhardt 1999; Goldblatt *et al.* 1989), *Nivenia* (Goldblatt & Bernhardt 1990), *Romulea* (Goldblatt *et al.* 2002), *Lapeirousia* (Goldblatt *et al.* 1995) and *Gladiolus* (Goldblatt & Manning 1998; Goldblatt *et al.* 1998a, 1998 b).

In addition to *Apis mellifera*, visitors to *Moraea* in the present survey, included a number of taxa, listed below.

- Melittidae: *Rediviva longimanus* which obtains oils from the long spurs of *Diascia longicornis* (Scrophulariaceae), and an undescribed polyphagous species of *Melitta*.
- Halictidae: species of *Lasioglossum* and *Patellapis* which more commonly visited *Herrea* (Aizoaceae: Mesembryanthema).
- Apidae: *Anthophora (Heliophila) wartmanni* (Anthophorini), which was most commonly visiting Asteraceae.
- Megachilidae: two polyphagous species – *Plesianthidium (Spinanthidium) neli* (Anthidiini) and a species of *Hoplitis* (*Anthocopa*) (Osmiini).

One of the most widespread bee–pollinated species of nectar-producing *Gladiolus* in the study area is *Gladiolus orchidiflorus*, which is found from the Cape Peninsula in the south to southern Namibia in the north and eastwards across Bushmanland and the Karoo to Kimberley and Fauresmith, but not in the southeast (Goldblatt & Manning 1998). During the present study, at a site in Namaqualand, it was found to be repeatedly visited by females of two polyphagous species of *Amegilla: A. obscuriceps* and *A. spilostoma* (Apidae: Anthophorini). Both these species were recorded by Goldblatt *et al.* as being visitors to *Gladiolus*, but not *G. orchidiflorus,* for which they recorded only *Anthophora (Pygnanthophora) diversipes* (Anthophorini). Struck (1994) made observations on visitors to *G. orchidiflorus* near Springbok, Namaqualand, where he recorded *Amegilla niveata* (Anthophorini) and *Plesianthidium (Spinanthidium) calvini* (Anthidiini). It seems likely that a wide range of *Amegilla* and *Anthophora* can be expected to visit this species of *Gladiolus* to obtain nectar.

Other monocots visited by bees are listed below:

- some *Albuca* spp. (Hyacinthaceae) by polyphagous Megachilidae;
- *Wachendorfia* sp. (Haemodoraceae) by polyphagous Apidae;
- *Bulbinella latifolia* (Asphodelaceae) by *Apis mellifera*;
- and *Bulbine frutescens* (Asphodelaceae) by polyphagous Megachilidae, most frequently *Megachile (Crieghtonella) dorsata*.

Visits by pollen wasps to monocots are unusual, in fact only *Aloe striata* (Asphodelaceae) and *Ferraria cf. divaricata* (Iridaceae) were recorded as receiving visits from these wasps. *Aloe striata* in the southern Great Karoo was visited abundantly by *Quartinia antigone* (a sample of 24 females and five males having been taken in a half hour), a species for which no other flower visiting records are known.

Ferraria is generally considered to be attractive only to flies (Cowling & Pierce 1999; Manning & Goldblatt 2001; Scott-Elliot 1891; Vogel 1954) or flies and small beetles (de Vos 1979). However, in the present study, *F. cf. divaricata*, at two widely separated sites, was being visited solely and repeatedy by female pollen wasps: in the foothills of the Kamiesberg by *Celonites capensis*, a widespread Karoo species; and in the Richtersveld by *Jugurtia koeroegabensis*, a narrowly endemic species. Neither of these wasps is restricted to *Ferraria*. Both are unusually polyphagous for pollen wasps, *C. capensis* having been recorded from flowers of six additional families and *J. koeroegabensis* from four.

Few species of wasps were found to visit any species of monocots, apart from *Asparagus suaveolens* (Asparagaceae), which they visit abundantly in the southeast. Five species of pompilids, three species of tiphiids, and one species each of scoliids and sphecids were recorded visiting *A. suaveolens*.

EUDICOTS

Proteales

Proteaceae

Proteaceae are not well represented within the study area, being Fynbos rather than Karoo plants. However, in the Clanwilliam and Nieuwoudtville areas, at the interface between karroid and fynbos scrub two species of Proteaceae (in fynbos) were sampled for flower visitors. One was the dusky–pink flowered *Paranomus bracteolaris*, growing west of Nieuwoudtville near the edge of the escarpment and in the hills to the west of Clanwilliam. The other was a species of *Leucadendron*, with relatively large brilliantly yellow female 'cones' held within broad yellow involucral leaves, growing west of Clanwilliam near Graafwater.

In the present study *P. bracteolaris* was being visited, at both of the above-mentioned sites, by bees of the families Apidae and Colletidae and wasps of the family Tiphiidae. Of particular interest are the colletids, *Scrapter erubescens* (Clanwilliam and Nieuwoudtville), also recorded from the *Leucadendron* (described above), and *Scrapter fuliginatus* (Clanwilliam). These are the only known records of flower visiting for these bees (Eardley 1996), suggesting that there may be an association between these bees and Proteaceae.

The apids were *Apis mellifera*, which were abundant visitors, and – uncommonly – *Amegilla spilostoma*, a polyphagous species (recorded from 15 plant families) with a wide distribution from the eastern limits of the Nama Karoo through to the west. The tiphiids – four species of *Mesa* and one of *Tiphia* at Nieuwoudtville, and one species of *Mesa* at the Clanwilliam site – can be expected to be polyphagous.

The *Leucadendron* species (described above) was also visited by a polyphagous cleptoparasitic bee, *Sphecodes* sp. (Halictidae), and 10 species of wasps of the families Pompilidae, Crabronidae, Philanthidae, Scoliidae and Tiphiidae. The crabronid wasps were *Oxybelus peringueyi*, *Oxybelus ruficaudis, Dasyproctus immitus* and *Dasyproctus ruficaudis*. They were probably casual visitors as the last three, at least, are polyphagous and widespread species. The scoliid, *Cathimeris (Cathimeris) capensis*, and the tiphiids – two species of *Mesa*, shared with *Paranomus bracteolaris* – can be expected to be polyphagous. The records of a single male each for the pompilids *Paracyphononyx frustratus* and *Psammoderes mimicus* and for a philanthid, *Philanthus capensis*, are probably of little consequence.

Rebelo (1995) states that some species of *Leucadendron* "are visited by a number of beetles; and that most of the genera (of Proteaceae) with smaller flower heads are visited by a variety of beetles, flies and wasps". It is clear that, in the light of the findings reported in the present survey, this statement can be expanded to include bees.

CORE EUDICOTS

Caryophyllales

In the study area, plants of six families of Caryophyllales, Aizoaceae, Amaranthaceae, Molluginaceae, Nyctaginaceae, Plumbaginaceae and Portulacaceae, were recorded as receiving visits from aculeates.

Amaranthaceae

Amaranthaceae form a notable component of the vegetation of northern Namaqualand and Namibia. Preliminary palyonological evidence from Eksteenfontein in the Richtersveld suggests that they were a previously predominant element before Aizoaceae (Mesembryanthema) took over in the early Holocene (Scott *et al.* 1997).

Several species of *Hermbstaedtia* – most notably *H. glauca* in the Richtersveld and *H. odorata* in Namibia – are attractive to wasps and bees. They were recorded as receiving visits from 7% of the total number of species: 42 wasps and 24 bees. One species of pollen wasp was recorded. Its visits were occasional and casual.

Amongst the wasps the most numerous species were Nyssonidae, of which 17 species were recorded: five species of *Bembecinus* and one each of *Bembix* and *Stizus* from *H. glauca*; and three species of *Bembecinus*, six of *Bembix* and one each of *Handlirschia*, *Stizus* and *Stizoides* from *H. odorata*.

A number of other other wasps were recorded visiting *Hermbstaedtia* spp.: seven species of Sphecidae and two species each of Chrysididae, Eumeninae (Vespidae),

Philanthidae and Scoliidae. These are all polyphagous. With the exception of Andrenidae, all bee families were represented amongst the recorded visitors to *Hermbstaedtia*. The family with the highest number of species represented was Megachilidae. All these are polyphagous.

Aizoaceae (including Mesembryathemaceae)

The family Aizoaceae has been variously delimited. In the present account the assessment of Bittrich & Hartmann (1988) is followed. The family is seen to consist of five sub-families arranged in two groups: one group, named Mesembryanthema, constituted of the Rushioideae and Mesembryanthemoideae; and the other without a formal taxonomic rank – referred to here as non–Mesembryanthema – constituted of Aizooideae, Sesuvioideae and Tetragonioideae.

The distribution of Mesembryanthema is centred in southwestern Africa (Hartmann 1991) whereas non–Mesembryanthema is cosmopolitan.

The Aizoaceae sampled for insect visitors were, in the main, shrubby or semi-prostrate species. None of the 'miniature' or 'cryptic' species was included. The flowers of the species of Mesembryanthema were either of the carpet or cone forms of Hartmann (1991) or of the cup form of Gess (1996). Recess flowers were not represented. However, Struck (1995) noted that the concealed flowers of *Dactylopsis digitata* in the Knersvlakte, Namaqualand, are visited by *Quartinia*.

Over the entire study area, 234 species (98 species of bees, 60 species of pollen wasps and 76 species of wasps, i.e. 25.24% of all of the species of aculeates recorded visiting flowers) were collected on flowers of Aizoaceae. Of these 234 species, 183 species were on Mesembryanthema and 80 species on non–Mesembryanthema. Less than 10% were visiting both Mesembryanthema and non-Mesembryanthema. A south – north shift is apparent. In the south 143 species were recorded visiting Mesembryanthema but in the transition (northern Succulent Karoo, north and south of the Orange River) and the north, only 31 species were recorded. By contrast, only 21 species were recorded visiting non–Mesembryanthema in the south and transition area (northern Succulent Karoo, north and south of the Orange River) but 57 species were recorded in the north. Thus, although there is a marked fall off in the number of species visiting Mesembryanthema on a south – north gradient, there is an increase in the number of species visiting non–Mesembryanthema.

Of the bee species, for which flower visiting records were obtained, 23.17% were collected on Aizoaceae. Species recorded from flowers of Aizoaceae – both Mesembryanthema and non-Mesembryanthema – represented all bee families: Andrenidae (4): Apidae (35); Colletidae (10); Halictidae (21); Megachilidae (21); and Melittidae (7). Some of these species show a considerable range of dependence on Aizoaceae and therefore a considerable range of dependability as visitors to flowers of this family. *Othinosmia (Othinosmia)* sp. A has been collected from flowers of these plants from eastern Nama Karoo, southern Great Karoo, the Olifants River Valley, and Namaqualand through to northern Richtersveld. The only other record for this bee was of one casual visit to *Grielum* (Neuradaceae). The flower preference of this species is in contrast to that of eight species of *Othinosmia (Megaloheriades)*, which restrict their visits almost entirely to Asteraceae. Several species of Colletidae in the southwest, Melittidae in the northern Richtersveld, and Fideliinae (Megachilidae) in the southwest and northwest, appear to be restricted to Aizoaceae, in particular Mesembryanthema. Unlike *O. (Othinosmia)* sp. A, these species have very limited distributions, being narrowly endemic.

Other species of bees visiting Mesembryanthema are polyphagous and therefore not dependent nor dependable visitors. A notable example is *Amegilla niveata*, a widespread species throughout the entire area both south and north, and almost as catholic in its flower visiting as *Apis mellifera*, having been recorded from flowers of 20 plant families.

As a group, pollen wasps show an exceptionally high preference for Mesembryanthema, 46.51% of species having been recorded from these flowers. They are associated with Mesembryanthema throughout their range and that of these plants. However, the majority of masarine/mesem associations are found in the southern region of the study area (Gess & Gess 2004a). Eight species of *Ceramius* variously distributed south of the Orange River, are dependent on Mesembryanthema and are therefore dependable visitors to a wide range of mesems. Five species of *Jugurtia* have been recorded from Aizoaceae. Two of these species are apparently dependent on Mesembryanthema and the other three species visit, in addition, a limited range of other families. Thirty eight species of *Quartinia* (presently constituted of *Quartinia, Quartinioides* and *Quartiniella*) visit Mesembryanthema and 65% of these species have been collected only, or predominantly, from these flowers. Three species of *Celonites* have been recorded from Mesembryanthema but these plants are not their primary forage plants.

South of the Orange River there appear to be no pollen wasp species dependent on non-Mesembryanthema. However, north of the Orange to the Kunene, *Ceramius damariuus* – the only species of *Ceramius* found in Namibia – provisions with pollen and nectar from these flowers by preference. When the favoured plants are in short supply, *C. damariuus* will, however, visit flowers from other familes for obtaining nectar.

Amongst the wasps, 20.27% of the species collected on flowers were recorded from Aizoaceae. Most of these were from non-Mesembryanthema. Included were representatives of all families. All of these species are polyphagous. Some species of scoliids are common and expected visitors to some large-flowered mesems.

Although the overall number of species visiting Mesembryanthema is large, at any one time and at any one place the number of species visiting these is usually small. Most of the bee visitors are polyphagous and few species are ever numerous visitors. Specialist species, however, when present, are usually numerous. Similarly, the specialist pollen wasp visitors, when they are present, are commonly very numerous. The most dependable and

frequent pollinators can be expected amongst the specialist bees and pollen wasps. However, it is likely that amongst the polyphagous bees some provide a 'back-up service'. Of the wasp visitors, only scoliids are likely pollinators.

A minority of Mesembryanthema, particularly those with dark colours, are not attractive to bees, pollen wasps or wasps. These, mostly, attract monkey beetles (Scarabaeidae: Hopliini) of the genera *Anisonyx* and *Peritrichia*, which are likely pollinators in both the west and the east.

Molluginaceae

The genera presently grouped as the family Molluginaceae have previously been variously included in the Phytolaccaceae and the Aizoaceae (non-Mesembryanthema). Though present and sampled throughout the study area, Molluginaeeae, like Aizoaceae: non-Mesembryanthema, are a more dominant element of the flora and are more frequently visited by bees, pollen wasps and wasps in the northern region than in the south. In the present study, four genera – *Gisekia, Limeum, Coelanthum* and *Corbichonia* – were sampled. The flowers are small and open, unspecialised in structure and mostly grouped to form heads. Visits by 70 species (19 species of bees, five species of pollen wasps, 46 species of wasps and, infrequently *Apis mellifera*), i.e. 7.35% of the species recorded visiting flowers, were collected from flowers of Molluginaceae. As the quantity of nectar obtainable from a single flower is small, visitors seeking nectar are likely to move from flower to flower. As the flowers are small and simple, all such visitors are potential pollinators.

Amongst the bees no specializations, expected visitors, or dependable visitors were evident. However, some bee taxa were relatively widely encountered visitors to Molluginaceae: panurgines were recorded from *Limeum, Gisekia* and *Corbichonia* in Namibia and from *Limeum* in southern Kalahari; and nomiines (Halictidae) from *Limeum* and *Gisekia* in western Namibia and from *Limeum* in the extreme southeast of the Nama Karoo and in southwestern Namibia.

The five species of pollen wasps fall into the categories 'expected' and 'casual'. The expected visitors are *Priscomasaris namibiensis* and a *Quartinia* species, which were repeatedly found only in association with *Gisekia* and *Limeum* in northwestern Namibia. *Ceranius damarinus* is an 'occasional' visitor, but shows a preference for Aizoaceae: non-Mesembryanthema, only visiting other flowers when its favoured flowers are in short supply. Occasional visitors between Clanwilliam and Graafwater are *Celonites wahlenbergiae* and *Celonites bergenwahliae*. These species show a preference for *Wahlenbergia* (Campanulaceae), but are not restricted to these plants. They occasionally visit the flowers of *Coelanthum* in the afternoon, which is when they open.

Of the wasps, 46 species from ten familes were collected from flowers of Molluginaceae: Nyssonidae (10); Crabronidae (9); Philanthidae (7); Pompilidae (6); Chrysididae (6); Sphecidae (2); Scoliidae (2); Tiphiidae (2); Vespidae (Eumeninae) (1).

These wasps are all polyphagous and none can be said to be dependent on Molluginaceae. However, *Limeum* species are undoubtedly an important nectar source for the larrines (Crabronidae) and nyssonids throughout the study area and, in all probability, these wasps provide a pollination service.

Nyctaginaceae

Although Nyctaginaceae are widespread in the arid areas, during the eourse of the present study only one species, *Boerhavia deserticola*, was encountered in flower. At a single site in northwestern Namibia on the desert fringe, where numerous plants were in flower in a dry drainage channel, these plants were receiving visits from six species (three bees, two pollen wasps and one wasp).

The three bees were polyphagous speeies: *Meliturgula haematospila* (Andrenidae), *Nomia (Acunomia) epileuca* (Halictidae) and *Coelioxys afra* (Megachilidae).

One of the pollen wasps was a species of *Quartinia* (formerly *Quartinioides*) which, however, was most abundantly found visiting the flowers of *Zygophyllum* species, in particular *Z. simplex*. The other was *Celonites gariepensis*, otherwise always found in association with *Peliostomum, Aptosimum* and *Anticharis* (all Scrophulariaceae) from northern Riehtersveld through southern and western Namibia. The visits to *B. deserticola* were casual and oceasional in nature and apparently only made by males.

The wasp, *Kohlia cephalotes* (Nyssonidae), was the most abundant of the visitors; however, at this and at other sites on the inland fringe of the desert, it was found more abundantly visiting *Zygophyllum simplex* (Zygophyllaceae).

Thus, although flowers of *B. deserticola* are clearly attractive to aculeates, none of those observed showed a marked preference for these flowers.

Plumbaginaceae

Plumbaginaceae is represented in southern Afriea by three genera: *Plumbago,* with slender tubular flowers; *Dyerophytum,* with more funnel-shaped tubular flowers; and *Limonium*, with petals separate or only fused for a short distance. Only the flowers of *Limonium* are suited to visitation by aculeates. The flowers of the other two genera appear to be visited solely by butterflies. Visits by insects to *Limonium* were observed only at Karoo Poort to the south of the Tankwa Karoo. Here, flowers of a violet-flowered *Limoniuu* were being visited occasionally. One bee and three species of pollen wasps were recorded. The bee was a single female of *Halictus* sp. A *cf. jucundus*; otherwise recorded from Asteraceae (from eastern Nama Karoo, southern Great Karoo, Little Karoo and Namaqualand) and from six other families.

In the course of a day, two females of *Celonites promontorii* were recorded from *Limonium*. This was surprising, as this wasp appears otherwise to specialize in visiting Asteraceae, having been recorded from flowers of this family from the eastern Nama Karoo, southern Great Karoo, Little Karoo and Namaqualand. The other two pollen wasps were a female of *Quartinia niveopicta* – otherwise recorded by Turner (1939) from Mesembryanthema – and five females of *Quartinia* sp. (*Quartinioides* sp. J), which is also otherwise associated with Mesembryanthema. More recently (since elosing the eatalogue for analysis) *Quartinia* has been found by the authors visiting

Limonium on the south coast to the west of Mossel Bay.

Portulacaeae

The only records of aculeate visits to Portulacaceae were for the succulent shrub *Portulacaria afra*, a dominant shrub in some areas of the southeast. The small, massed flowers appeared to receive few visits from aculeates. Those recorded were all by eumenines, *Antepipona* and *Zethus*.

Saxifragales

Crassulaceae

Crassulaceae is one of the families listed by Cowling & Hilton Taylor (1999) as among the largest in the Karoo Biome. Although few cases of bee, pollen wasp and wasp activity on flowers of this family were noted, observations for *Crassula, Cotyledon* and *Tylecodon* are of interest. In all three genera, the flowers patronised have a tubular corolla and are held either erect or hanging down.

Crassula dichotoma – an erect annual herb, 2-15 cm high, with striking yellow flowers marked with reddish orange at the lip – is commonly found growing together with *Wahlenbergia* spp. in sandy areas from the southwestern Cape to Namaqualand. Flower visitors were observed on two occasions only. At SorsSors in the Kamiesberg the flowers were being repeatedly visited only by *Haplomelitta (Prosamba) griseonigra* (Melittidae), for which no other flower visiting records are available. The second occasion was on the east bank of the Clanwilliam Dam where the flowers were being visited for nectar by a nesting female of *Celonites wahlenbergiae* (Masarinae). This species is particularly associated with *Wahlenbergia* spp. (Campanulaceae) but does visit flowers of other families for nectar for use in provisioning its nests and in cell construction (Gess & Gess 1992). Both the bee and the wasp, in size and behaviour, would be likely pollinators.

Little has been recorded concerning the visitors to the flowers of *Tylecodon* spp. The widespread *Tylecodon paniculatus* has dull red-streaked flowers borne horizontally on scarlet, robust inflorescence stems characteristic of bird pollinated plants and is, indeed, sunbird pollinated (Gess *et al.* 1998). *Tylecodon hallii* a narrowly endemic species of northern Richtersveld and southern Namibia has erect greenish yellow flowers. These were observed in two consecutive years and were found to be visited solely and in large numbers by a pollen wasp, *Masarina tylecodoni*, which appears to be restricted to visiting these flowers and – in fit and behaviour – to be suited to be their pollinators (Gess *et al.*1997 & 1998). Visitors to a third species of *Tylecodon, T. cacalioides*, were observed in the western Little Karoo by Robert Gess in two successive years. He noted that the bright yellow flowers of this species were not attracting aculeates but a long-proboscid horse fly, *Philoliche (Phara) tumidifacies* (Tabanidae) (R.W.Gess 2001).

The flowers of *Cotyledon* species are mainly pendulous and the length of the tube is variable. For example, the reddish flowers of *C. orbiculata* are about 2.5 cm long, whereas those of the yellow flowered *C. campanulata* are about half this length. The flowers of *C. orbiculata* are visited by long billed sunbirds and also by *Xylocopa* (Apidae: Xylocopinae) and *Lipotriches* sp. B (Halictidae). The halictid bees are small enough to enter the flowers but even the smaller species of *Xylocopa*, such as *X. sicheli*, are unable to reach the nectar 'legitimately' and 'steal' it by puncturing the corolla tube near the base. Both bees are, however, legitimate visitors of *C. campanulata* and are amongst its potential pollinators.

ROSIDS

Zygophyllaceae

Zygophyllaceae are most abundant in the tropics and sub-tropics, mainly in hot, arid regions with alkaline soils, and it is therefore not surprising that in southern Africa the greatest species diversity and the greatest abundance of individual plants is encountered in the western semi-arid to arid areas of this region. Although not one of the ten largest families in the Karoo, the genera *Zygophyllum, Tribulus, Sisyndite* and *Augea* are amongst those that characterise the vegetation of these areas (Cowling *et al.* 1997; Dean & Milton 1999). After rain these plants produce an abundance of usually showy (mostly yellow or white) flowers that offer rich rewards to flower visitors. The only species to have been the principal focus of a published study of flower visitors appears to be *Zygophyllum simplex*, which was the subject of an investigation at the Namib Desert Research Institute, Gobabeb, Namibia (Wharton 1980).

In the present study, 139 species of aculeates (71 species of bees, 17 species of pollen wasps and 51 species of wasps), i.e. 14.99% of the species recorded visiting flowers, were collected on flowers of Zygophyllaceae. Taken as a group, Zygophyllaceae were visited by all bee families, pollen wasps and all wasp families, with the exception of Ampulicidae and Astatidae.

Of the *Zygophyllum* species sampled, nine were identified:

- *Z. clavatum*, a mound-forming species with small, white flowers, sampled in Namibia at Oranjemund and Lüderitz;
- *Z. cylindrifolium*, a stringy dwarf shrub with small, white flowers sampled in drainage channels in the northern Namib between Usakos and Rössing, Uis and Henties Bay and the Gaub and Kuiseb passes;
- *Z. divaricatum*, a shrubby lax species with relatively large, yellow flowers, sampled in Namaqualand in the Kamiesberg and near Springbok;
- *Z. meyeri*, a lax shrubby species with relatively large, yellow flowers, sampled in Namaqualand in the northern Richtersveld and by Struck (1994) in the Goegap Reserve near Springbok;
- *Z. cf. morgsana*, a shrubby species with relatively large, yellow flowers, sampled east of Nieuwoudtville;
- *Z. prismatocarpum*, a stringy shrubby species with small, white flowers, sampled in drainage channels in northern Richtersveld and across the Orange River in southern Namibia;
- *Z. retrofractum*, a compact shrubby species with small, creamy white flowers, sampled in the Little Karoo, southern Great Karoo and by Struck (1994) in

the Goegap Reserve, in Namaqualand;
- *Z. simplex*, a succulent annual with small, yellow flowers, forming miniature shrublets which become mat-like or form mounds where sufficient moisture is available, sampled in northern Richtersveld and at numerous sites throughout the area designated as Karoo Biome, on the eastern dry Savanna fringes and across the Namib Desert down to the coast and north along the coast from Walvis Bay;
- *Z. stapffii*, a mound-forming species with relatively large succulent leaves and relatively large, white flowers, sampled on the Central Namib coast.

In Namaqualand, south of the Richtersveld, the three shrubby species with relatively large, yellow flowers (*Z. divaricatum, Z. meyeri* and *Z. morgsana*) were solely visited by polyphagous bees, including *Apis mellifera*. The visitors were species of Anthophorini (Apidae: Apinae), notably including seven species of *Anthophora (Pyganthophora)* (but not any other subgenera of *Anthophora*) and Megachilidae, notably five species belonging to the Anthidiini and – at Springbok and Nieuwoudtville, each – a single species of *Melitta* (Melittidae). The preference shown by *A. (Pyganthophora)* for Zygophyllaceae supports the earlier findings of Gess & Gess (1996). Of the three species, the widespread *Z. meyeri* was also sampled in northern Richtersveld. Here it was visited almost exclusively by pollen wasps and colletid bees, which are amongst the visitors to *Zygophyllum prismatocarpum*, a much more visited species in this area where it was receiving visits from six species of pollen wasps and *circa* ten species of Colletidae. These associations are particularly interesting as, in the more southerly areas, no pollen wasps have been recorded from Zygophyllaceae and only once was a colletid *(Scrapter nitidus)* recorded. In addition, *Z. prismatocarpum* was visited by three species of melittids (one of which is the species of *Melitta* recorded from *Zygophyllum* in the Nieuwoudtville area), two species of *Fidelia* (*Parafidelia)* (Fideliinae), a species of *Lasioglossum* (Halictidae), and *Bembecinus hyperocrus* (Nyssonidae). The presence of a species of *Bembecinus,* although polyphagous, is of interest because *Bembecinus rhopaloceroides* was the principal visitor to *Zygophyllum retrofractum* in the Little Karoo and southern Great Karoo and a *Bembecinus* species was the only visitor to *Z. retrofractum*, recorded by Struck (1994) at Springbok.

From northern Richtersveld northwards through Namibia, the widespread annual *Z. simplex* is an important resource. In the present study 15 species of bees (including *Apis mellifera*), five species of pollen wasps, and 21 species of wasps from six families were recorded. Although Wharton (1980) recorded a smaller number of flower visitors, bees, pollen wasps and wasps were represented in similar proportions.

The northern coastal and desert perennial species, *Z. clavatum, Z. stapffii* and *Z. cylindrifolium*, are similarly attractive to bees, pollen wasps and wasps, although they never appear to attract either the diversity or numbers found visiting *Z. simplex*.

Interestingly, at Oranjemund just north of the Orange River, Colletidae are amongst the most frequent visitors just as they are to *Zygophyllum* species in northern Richtersveld to the south of the Orange River.

Tribulus species are widespread in the more arid areas and are striking to the north where mass flowering takes place in the more sparsely vegetated areas, particularly where the ground has been disturbed by trampling. They are among the plants with staggered germination, in which not all the seeds produced by an individual are expended in a single attempt at establishment (van Rooyen 1999). These plants are ideally suited to areas where opportunistic response to irregular rainfall is a requirement.

Tribulus appears to be visited by a far smaller range of aculeates than *Zygophyllum*, particularly if comparison is made with *Z. simplex* – another widespread, and often abundant, low-growing annual of the northern arid areas. At the family level, some noticeable differences were the absence of Colletidae and pollen wasps from *Tribulus*.

North of Sesfontein, at several sites on the road to Opuwa, *Tribulus* was being most abundantly visited by a social apid, *Meliponula (Meliplebeia) beccarii* (Meliponinae).

Sisyndyte is a monospecific genus, endemic to the northern Cape and Namibia. In the present study, *Sisyndite spartea* was sampled for flower visitors in the northern Richtersveld south and north of the Orange River, where it was found to be visited almost solely and repeatedly by Apidae – *Xylocopa* spp. and honey bees. However, to the south (70 km east of Port Nolloth) Rozen (1977) recorded that it was visited by *Fidelia (Parafidelia) pallidula* (Fideliinae), an association also recorded by Whitehead (1984).

Geraniales

Geraniaceae

Geraniaceae are poorly represented in the present study. However, the available information on visitors to the flowers of *Pelargonium*, has been assembled and analysed by Struck (1997), making it possible to comment usefully on additional records from the present study. Struck examined data for 208 Pelargonium taxa (species, subspecies and varieties), which included some records of the present authors. He concluded that of these *Pelargonium* taxa, 60% are bee-pollinated, 25% long-proboscid hovering fly-pollinated, 7% butterfly-pollinated, 2-4% hawkmoth-pollinated, and 1% are probably bird-pollinated. Records subsequently collected and records of Jacot Guillarmod (from specimen labels) add to the knowledge of the association between pollen wasps and Geraniaceae.

Jacot Guillarmod sampled *Pelargonium myrrhifolium* (Sect. Myrrhidium) near Oudtshoorn in the Little Karoo and recorded ten polylectic aculeates as flower visitors: four species of bees, one species of pollen wasp and five species of wasps. These were *Colletes fasciatus* (Colletidae), *Hoplitis (Anthocopa)* sp. A (Megachilidae: Osmiini), *Epeolus amabilis* (Apidae: Nomadinae), *Amegilla niveata* (Apinae: Anthophorini), *Celonites capensis* (Masarinae), three species of *Alastor, Eumenidopsis bacilliformis* and a speeies of *Stroudia* (all Eumeninae). This adds considerably to the records cited in Struck (1997): a single species of Megachilidae recorded by himself and a fly (Bombyliidae) Vogel (1954) and Jacot Guillarmod (from label data).

For the present study, two species of *Pelargonium* – attracting appreciable numbers of aculeates – were sampled: *Pelargonium capitatum* (Sect. Pelargonium) in two successive years between Clanwilliam and Graafwater to the west, and *Pelargonium klinghardtense* in three successive years in northern Richtersveld.

The small pink flowers of *P. capitatum* were visited by the following insects:

- four polyphagous bees – *Amegilla spilostoma* and *Tetraloniella minuticornis* (both Anthophorini), *Megachile (Chalicodoma) karooensis* (Megachilini), and *Hoplitis (Anthocopa)* sp. A (Osmiini);
- two pollen wasps most closely associated with, but not restricted to, *Wahlenbergia* (Campanulaceae) (*Celonites wahlenbergiae* and *Celonites bergenwahliae*);
- bombyliid flies;
- and a lycaenid butterfly, which was drinking nectar but also laying eggs, its caterpillars being *Pelargonium* feeders.

The flowers of *P. klinghardtense* (white with the opening to the 4 mm deep hypanthium red) were visited abundantly and principally by pollen wasps. The only other visitors recorded were a megachilid and a tabanid: *Mesomyia (Erodiorhynchus) edentula*, which is commonly and widely found associated with orange and yellow daisies (ligulate Asteraceae, *Didelta, Dimorphotheca* and *Osteospermum*). The most abundant pollen wasps were *Jugurtia codoni* – which at a different site was abundant on *Codon* (Boraginaceae) – and *Masarina mixtoides*, which is narrowly polyphagous but most often associated with *Wahlenbergia* (Campanulaceae). Other less common pollen wasp visitors were *Celonites promontorii*, a species most often associated with Asteraceae, and a *Quartinia* species.

It seems possible that pollen wasps, while not being important visitors to most species of *Pelargonium*, may well be of importance as pollinators of some species, for example *P. klinghardtense*, which – judged by the number and nature of the visits – is an important source of nectar for these visitors.

Cream-and pink-flowered *Sarcocaulon* species were observed in Namaqualand – in the Springbok area and in northern Richtersveld – and in southern Namibia from east of Oranjemund to south of Rosh Pinah. They were rarely abundantly visited. The most widespread visitor appeared to be *Hoplitis (Anthocopa)* sp. A, listed above as an occasional visitor to *P. myrrhifolia* and *P. capitatum*. It was also collected from flowers of Asteraceae in the eastern Nama Karoo, the Olifants River Valley and Namaqualand and singly from *Homeria* (Iridaceae) and *Ballota* (Lamiaceae) in Namaqualand. Petal nests of this bee were found in snail shells from sites north and south of the Orange River. The petals used were from a pink-flowered *Sarcocaulon*. The pollen obtained from a nest was examined microscopically and found to match that of *Sarcocaulon* (Gess & Gess 1999).

East of Oranjemund several plants of a cream–flowered *Sarcocaulon* were being visited by numerous individuals of a *Quartinia* species, which, at the same site, was also visiting flowers of Aizoaceae, Asteraceae and occasionally *Aptosimum* (Scrophulariaceae).

Only *Apis mellifera* has been observed visiting the widespread exotic weed *Erodium circutarium*.

EUROSIDS I

Celastraceae

In the Celastraceae, *Maytenus* species are a notable component of the taller shrubby vegetation of drainage channels in the Nama Karoo and, when in flower in the early summer, are immediately apparent as they produce an abundance of small, white, heavily scented flowers. The species are variously attractive to aculeates. For example, in an area northwest of Grahamstown, *Maytenus linearis (Gymnosporia linearis)* attracts large numbers and a great diversity of aculeates. Forty seven species were collected: 40 species of wasps (a single species of Bradynobaenidae, six species of Crabronidae, two species of Mutillidae, two species of Nyssonidae, eight species of Philanthidae, nine species of Pompilidae, three species of Sphecidae, four species of Tiphiidae, three species of Eumeninae (Vespidae)) and seven species of bees (a single species each of Apidae and Colletidae, and five species of Halictidae). By contrast, *Maytenus deflexa (Gymnosporia buxifolia)*, which – to the human nose – has a rather unpleasant scent, attracts very few aculeates but an abundance of flies.

Cucurbitales

Cucurbitaceae

Cucurbitaceae are a feature of the more arid areas in the north. The flowers attract small numbers of a limited range of aculeates. Only seven species of bees were recorded, as listed below.

- Five polyphagous species: three Apinae (Apidae), *Amegilla niveata, Amegilla langi* and *Thyreus abyssinicus* (a cleptoparasite); a single species of Xylocopinae (Apidae) of the genus *Braunsapis*, and a single species of Nomiinae (Halictidae),*Nomia (Acunomia) epileuca*.
- Two casual visitors which are specialist visitors to other plant taxa: *Fidelia (Parafidelia) friesei* (Megachilidae), which is a specialist visitor of *Sesamum* spp. (Pedaliaceae); and *Meganomia binghami* (Melittidae), which is a specialist visitor of Papilionaceae.

Fabales

Two families of Fabales, Fabaceae and Polygonaceae, are represented in southern Africa. Both are visited by aculeates.

Fabaceae (Leguminosae)

Fabaceae is one of the largest plant families of the Karoo-Namib Region (Cowling & Hilton-Taylor 1999).

The flowers of Fabaceae taken as a whole, in the present study, were recorded as receiving visits from 322 species of aculeates (164 species of bees, 11 species of pollen wasps and 147 species of wasps), i.e. 34.74% of species recorded visiting flowers were collected on

Fabaceae, second only to the perentage of species collected on Asteraceae (Table 1). Due to distinct differences in flower morphology and therefore of flower visitors the three sub-families – Mimosoideae, Papilionoideae and Caesalpinoideae – will be considered separately.

MIMOSOIDEAE

Mimosoideae – shrubs to small trees, mostly associated with drainage channels – are common in all but the winter rainfall areas. They are visited by a great diversity of wasps (114 species, i.e. 30.04% of all the wasp species recorded from flowers) and to a far lesser degree by bees (only 28 species, i.e. 6.62% of all the bee species recorded from flowers). The ratio of wasps to bees visiting these plants is, therefore, approximately 4:1, a ratio that is very different from that for Papilionoideae and Caesalpinoideae (Figure 19). Only one individual male pollen wasp, *Jugurtia confusa* has been recorded visiting Mimosoideae. This was clearly only a casual visit.

The wasps,114 species, were from a wide range of families – Ampulicidae (1), Chrysididae (5), Crabronidae (7), Nyssonidae (7), Philanthidae (16), Pompilidae (16), Scoliidae (14), Sphecidae (14), Tiphiidae (7), and Vespidae (Eumeninae) (27). The bees were from families showing a relatively high overall diversity of choice: Andrenidae (one species), Halictidae (four species), Megachilidae (12 species) and Apidae (11 species). Colletidae and Melittidae, both of which show a markedly lower overall diversity of choice, were absent.

The flowers of Mimosoideae also attract a great diversity of other insects, notably butterflies and beetles, although wasps are their most species-diverse and numerous visitors.

PAPILIONOIDEAE

Shrubby and herbaceous, perennial and annual species of Papilionoideae occur throughout the study area, represented in this survey principally by *Crotalaria, Lotononis, Melolobium, Aspalathus, Lebeckia, Wiborgia,* and *Rafnia* (all Crotalarieae) and *Indigofera* (Indigoferae). Less common are *Tephrosia* (Tephrosieae), *Otoptera* (Phaseoleae), *Lessertia* (Galegeae), and *Cullen* and *Psoralea* (both Psoraleae).

A great diversity of bees (138 species, i.e. 32.62% of all the bee species recorded from flowers), were collected from flowers of Papilionoideae and a lesser diversity of wasps (64 species, i.e. 17.07% of all the wasp species recorded from flowers). The ratio of wasps to bees visiting these plants is, therefore, approximately 1:8, a reverse of the pattern obtained for Mimosoideae (Figure 19). Furthermore, 10 species of pollen wasps were collected from Papilionoideae as against the single male pollen wasp collected from Mimosoideae.

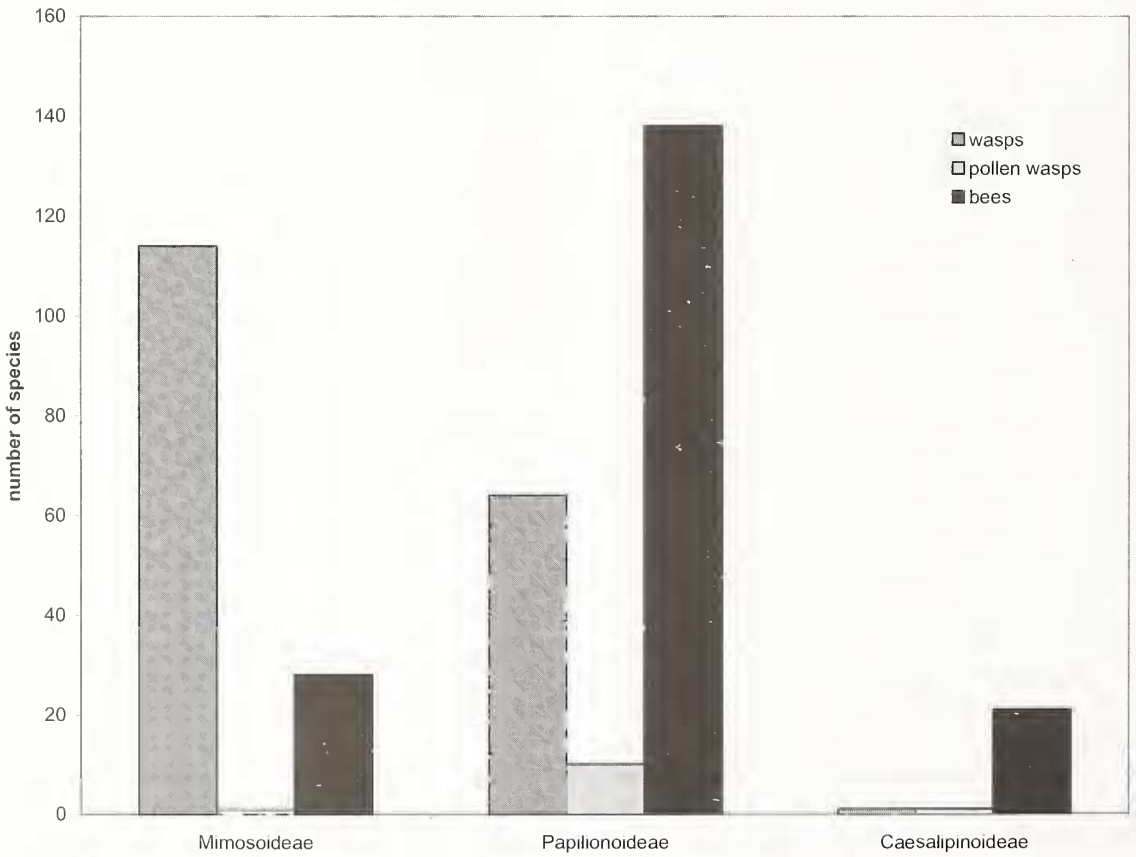

Fig. 19. Comparison of the complexes of wasps, pollen wasps and bees visiting the three subfamilies of Fabaceae.

Despite the far lower number of wasp species recorded from flowers of Papilionoideae as compared to that from flowers of Mimosoideae, the wasp family representation is the same. By contrast, the family representation for bee species visiting flowers of Papilionoideae is very different from that for bees visiting Mimosoideae. Whereas only the four bee families that show a high diversity of choice visit Mimosoideae, all these familes and the two remaining families – Colletidae and Melittidae – that show a low diversity of choice were recorded from Papilionoideae.

In an analysis of the visitors to Cape Crotalaricae (*Aspalathus, Lebeckia, Wiborgia* and *Rafnia* – all yellow flowered) all assemblages from the western, northern (Namaqualand), and eastern Cape were characterized by the presence of Megachilinae (Megachilidae) and Xylocopini (Apidae) or Anthophorini (Apidae). Masarinae (Vespidae) were represented in samples from *Aspalathus, Lebeckia* and *Wiborgia* in Namaqualand and from there south to the Cape and east to Ladismith in the western Little Karoo(Gess & Gess 1994a). Although not restricted to Polhill's Cape Group, the Megachilinae, Xylocopini and Anthophrini were considered to be potential pollinators. Two species of *Masarina* (Masarinae) are apparently restricted to *Aspalathus*, *Lebeckia* and *Wiborgia*, and are potential pollinators of the smaller-flowered species of these genera. Two species of *Ceramius* (Masarinae) are apparently restricted to *Aspalathus*. Within their distribution ranges they are the most dependable visitors and therefore the most dependable pollinators of this genus. *Apis mellifera* and Eumeninae (Vespidae) visit all four genera but are probably of little importance as pollinators. *Apis mellifera* is certainly able to obtain nectar from the smaller-flowered species without 'tripping' (opening the keel to expose the anthers and stigma) the flowers. Flower structure and visitor behaviour are dealt with in some detail by Gess (1996).

Although *Crotalaria* is the most widespread genus of Crotalariae, the Karoo and Cape Regions support a negligible representation (Polhill 1982). The genus was sampled wherever it was encountered throughout the study area. All species were yellow flowered. It was only in Namibia that any stands of appreciable numbers of plants were found. These were erect annual to short-lived-perennial plants. The species sampled and their distributions are listed below:

- *C. podocarpa*, a species of dry open sandy places where a little additional water collects, widespread with a distribution extending well east and north of Namibia to the Sahel;
- *C. damarensis*, a semi-arid to desert species extending from the Namib Desert across to Mozambique;
- and *C. argyraea*, a semi-arid to desert species,extending from Namibia into southern Angola.

The three above-mentioned species, which are superficially very similar in habit, were sampled wherever they were encountered from southern Namibia through the semi-arid and arid west to south of Opuwa in the Kaokoveld. At all sites they were visited frequently by a range of large Megachilini, nine species of *Megachile* having been recorded. In the area bounded by Omaruru, Palm and Khorixas additional abundant visitors were *Meganomia gigas* (Melittidae), an exceptionally large species, and *Nomia (Crocisaspidia) maculata* (Halictidae). Occasional visitors of particular interest were *Fidelia (Parafidelia) ornata* (Fideliinae) and a species of *Anthidium* (Anthidiini). To the south west of Helmeringhausen further occasional visitors were *Pseudapis cinerea* (Halictidae) and *Serapista rufipes* (Anthidiini). Throughout the area, the larger *Megachile* species, although polyphagous, are undoubted pollinators. Additional infrequent visitors were Apidae of which species of *Xylocopa* (Xylocopinae) and *Amegilla* (Anthophorini) would certainly be able to service the flowers. Although not as widespread, *Meganomia gigas* is an undoubted pollinator and, in the areas where it occurs, is probably more dependable, not having been recorded from any other flowers.

A fourth erect species, *Crotalaria virgultalis* – a Kalahari species that is broom-like in habit – was sampled at several sites in the southeast of Namibia, where it was flowering abundantly on the red sands. It was similarly being visited principally by a large species of *Megachile,* which is an undoubted pollinator.

Other Crotalarieae sampled in Namibia and Namaqualand were semi-prostrate, mat-forming species. These were also visited principally by Megachilidae. *Crotalaria dinteri* was sampled east of the Gamsberg, where it was visited by *Megachile*. In the Kamiesberg, *Lotononis bainesii* was sampled in two years at two sites and was repeatedly visited by *Megachile (Chalicodoma) murina*. This bee was also frequently represented in samples from Cape Crotalarieae: *Aspalathus* in southeastern Nama Karoo and in the west from the Olifants River, westwards, eastwards and northwards through Namaqualand; and *Lebeckia* and *Wiborgia* in the west. It was otherwise recorded from *Polygala* in Namaqualand and a single female was recorded from Lamiaceae. It would appear that this bee is closely associated with Fabales and in particular with Crotalarieae, regardless of plant form. It is of interest that it also visits flowers of *Polygala* (Polygalaceae).

Two species of Tephroseae with relatively large, pink flowers were sampled in Namibia. Both were visited solely by a limited number of large polyphagous bees:

- *Tephrosia burchellii*, in the southeast, was visited by *Meliturgula flavida* (Andrenidae: Panurginae), *Amegilla langi* and a species of *Ceylalictus* (Halictidae: Nomioidinae);
- *Tephrosia oxygona*, in the northwest, was visited by two of the same *Megachile* species – *M. (Maximegachile) maxillosa* and *M. (Gronoceras) felina cerberus* – which commonly visit *Crotalaria* in the same area.

Although not encountered in the present survey, it is of interest that *Fidelia (Parafidelia) ornata* (Megachilidae: Fideliinae) has been recorded from two species of *Tephrosia* (Whitehead 1984).

A single species of Phaseoleae, the desert pea, *Otoptera burchellii,* with large pink flowers, was sampled in the Grootberg, west of Kamanjab. It was being visited by *Amegilla calens, Xylocopa caffra, Xylocopa lugubris,* and *Megachile (Gronoceras) felina cerberus*, all of which would have the capability to be pollinators of the flowers. It is likely that in other areas it is visited by these and/or

other large Apidae and Megachilidae.

The Indigofereae sampled were all species of *Indigofera*, erect and mat-forming herbs and woody dwarf shrubs with small pink, reddish pink or orange flowers. The principal species are listed below:

- *I. alternans*, a pink or pinkish-orange flowered, semi-prostrate, mat formimg herb, sampled in six areas of southeastern Namibia and one in the southeastern Karoo;
- *I. auricoma*, a pink flowered, semi-prostrate herb, sampled at various sites on the desert margin from Aus to the Gaub Pass;
- *I. charlieriana*, a pink flowered herb, sampled in two areas of southeastern Namibia;
- *I. filipes*, a pink flowered, erect herb, sampled in four areas in southeastern, and one in northwestern, Namibia;
- *I. longispina*, a pinkish-red flowered, woody dwarf shrub, sampled in the Richtersveld to the south and north of the Orange River;
- *I. rautaneii*, an orange flowered dwarf shrub, sampled in the Grootberg Pass in northwestern Namibia.

The representation of bee taxa overall was as follows:

- three species each of Andrenidae and Apidae;
- five species of Melittidae;
- eight species of Halictidae (all Nomiinae);
- 24 species of Megachilidae (all Megachilinae) –

16 species of Anthidiini, five species of Megachilini, and three species of Osmiini.

Only one species of pollen wasp – a species of *Quartinia* – was collected on *Indigofera auricoma*, and that at only one of the four sites where this species was sampled. Visiting by wasps was generally uncommon.

Anthidiini were not only the most species diverse but also the most widely-encountered group, except in the southeast where only Megachilini were recorded. In most areas anthidiines can be said to be expected visitors and likely dependable pollinators.

Indigofera longispina was sampled in the Richtersveld National Park and north across the Orange River. In addition to being visited by Anthidiini in both areas it was also visited abundantly in the former area by two melittids: *Haplomelitta (Atrosamba) atra* (a species recorded widely in the west), and *Haplomelitta* sp. Neither of these two species appears to have been recorded from any other plants. All of the above-mentioned species are potential pollinators of *Indigofera longispina*.

In the Kalahari sand areas two other melittids – *Ceratomonia rozenorum* and *Meganomia binghami* – are frequent visitors to *Indigofera* species, the former having been recorded solely from *Indigofera* in that area.

The composition of the assemblage of bees from *Indigofera* as a whole is markedly different from that from Crotalarieae. This is illustrated by comparing the complex of visitors to *Indigofera* to the complex of visitors to *Aspalathus (Crotalarieae)* which has similarly-sized flowers (Figure 20). This is particularly striking when the tribal composition of Megachilidae visiting flowers of these two genera is compared. Whereas only five species of Megachilini were recorded from *Indigofera*, 19 species were recorded from *Aspalathus*. Sixteen species of Anthidiini were, however, recorded from *Indigofera* but only eight species from *Aspalathus*. Three species of Apidae were recorded from *Indigofera* as compared with eight species from *Aspalathus*. Furthermore, Masarinae – which are important visitors and pollinators of *Aspalathus* in the southwest – were entirely absent from samples from *Indigofera*, except for one sample from the northwest between the Gaub and Kuiseb passes.

Three species of *Lessertia* (Galegeae) were sampled. Two of these were from the southwest: *L. diffusa* in the Goegap Reserve, Springbok, and *L. cf. spinescens* at Wallekraal southwest of Springbok. Both were visited solely by Anthidiini. The third galegaeid plant *(L. macrostachya)* – a more robust, larger-flowered species, sampled in the Kalahari sands arca of Namibia – was visited principally by large species of *Megachile* and by *Meganomia binghami* (Melittidae).

Only four species of Psoraleae – *Psoralea pinnata* and *Psoralea oligophylla* in the southeast, *Psoralea* sp. in the Little Karoo, and *Cullen obtusifolia* near Augrabies – were sampled. The principal visitors were Apidae and Megachilidae.

CAESALPINOIDEAE

Caesalpinoideae were sampled only in the north. Three species were sampled for flower visitors: *Adenolobus pechuelii* (which has yellow and orange flowers), *A. gariepensis* (which has red flowers), and *Senna italica* (which has yellow flowers).

Adenolobus pechuelii was commonly encountered on rocky banks of relatively deep drainage channels in the northwestern desertic areas. It was sampled principally between the Gaub and Kuiseb passes and southwest of Büllsport, and at additional sites further north near Palm, Rössing Mountain, to the south between Alexander Bay and Port Nolloth, and at one site in southeastern Namibia at Gross Nabas. Sixteen species of bees were taken: Apidae (9), Halictidae (3), Megachilidae (3) and Andrenidae (1). Of these the most likely pollinators are the larger bees, three *Amegilla* spp. (Anthophorini), three *Xylocopa* spp. (Xylocopini), two large anthidiines (species of *Afranthidium* and *Trachusa*) and *Megachile (Maximegachile) maxillosa* (Megachilini). All except the anthidiines are broadly polyphagous.

A relatively polyphagous pollen wasp – a species of *Quartinia* that is apparently an opportunist – was an extremely abundant visitor at sites between the Gaub and Kuiseb passes. Its small size makes it unsuited to being a pollinator.

No wasps were found visiting *A. pechuelii* and the only visitor to *A. gariepensis*, which was encountered only at Rooibank on the lower reaches of the Kuiseb River, was a male *Philanthus triangulum* (Philanthidae).

Senna italica was only encountered in flower in the southern Kalahari and between Rehoboth and the Gamsberg Pass in Namibia. In all cases visitors were large Apidae. In the southern Kalahari what was taken to be a species of *Xylocopa* was in attendance. No voucher specimens were, however, obtained. This sight identification was most probably correct as *Xylocopa* species are frequent visitors to cultivated *Cassia* species. In Namibia *Amegilla atrocincta* and *Anthophora*

(Paramegilla) armata were frequent visitors. The flowers require to be buzzed as the anthers dehisce apically. All of these bees are of suitable size and weight to be pollinators.

Even taking into account the small number of Caesalpinoideae sampled, it is apparent that far fewer flower visitors are attracted to these flowers than to Mimosoideae and Papilionoideae (Figure 19).

Polygalaceae

Polygalaceae was placed together with Fabaceae in the Fabales by the Angiosperm Phylogeny Group (APG 1998). Unlike Fabaceae, Polygalaceae is not one of the families that characterizes the Karoo Biome, either in numbers of individual plants or in numbers of species. Indeed, of the southern African Biomes, it is only the Fynbos Biome which has large numbers of species of this family (Cowling et al. 1997).

In the present survey only two species of *Polygala* were sampled: *P. virgata* in the Goegap Nature Reserve, Springbok, and *P. hottentota* on a farm near Colesburg in the southeast.

In Goegap *P. virgata* is not uncommon in the hills in moist areas where there is water seepage. Sampled in two separate years, it was found to be visited solely by Megachilidae: two species of *Plesianthidium* (Anthidiini) – *P. (Carinanthidium) cariniventre* and *P. (Spinanthidiellum) volkmanni* – and four species of *Megachile* (Megachilini) – *M. (Maximegachile) maxillosa* and three species of *M. (Chalicodoma)*. The *Plesianthidium* species and the *Chalicodoma* species were most often encountered visiting the flowers of Papilionoideae in the Olifants River area and Namaqualand and *Megachile (M.) maxillosa* was a frequent visitor to *Crotalaria* (Papilionoideae) in Namibia.

Polygala hottentota, like *P. virgata*, was growing in an area where there was moisture seepage. It was visited by two species of *Megachile (Chalicodoma)* and *Xylocopa caffra* (Apidae: Xylocopinae).

All of the bees recorded from *Polygala* flowers are suited to being pollinators of these flowers.

Malpighiales

Euphorbiaceae

Euphorbiaceae, a family exhibiting a high degree of endemism, is listed by Cowling & Hilton-Taylor (1999) as the ninth largest family in the southern Karoo and Namaqualand-Namib domains of the Succulent Karoo and eighth in the Damaraland-Kaokoveld domain of the Nama Karoo. Few Euphorbiaceae observed appeared to be attracting visits from solitary wasps and bees, although several of the succulent, yellow 'flowered' species were visited by *Apis mellifera* in the southeastern Nama Karoo and Namaqualand. The exceptions, and there are surely others, were as follows: an annual herb, *Chamaesyce glanduligera*, commonly occurring in drainage channels in the Nama Karoo of Namibia and across the Namib Desert to the coast; and *Euphorbia mauritanica*, an erect perennial succulent with clusters of yellow flower-like

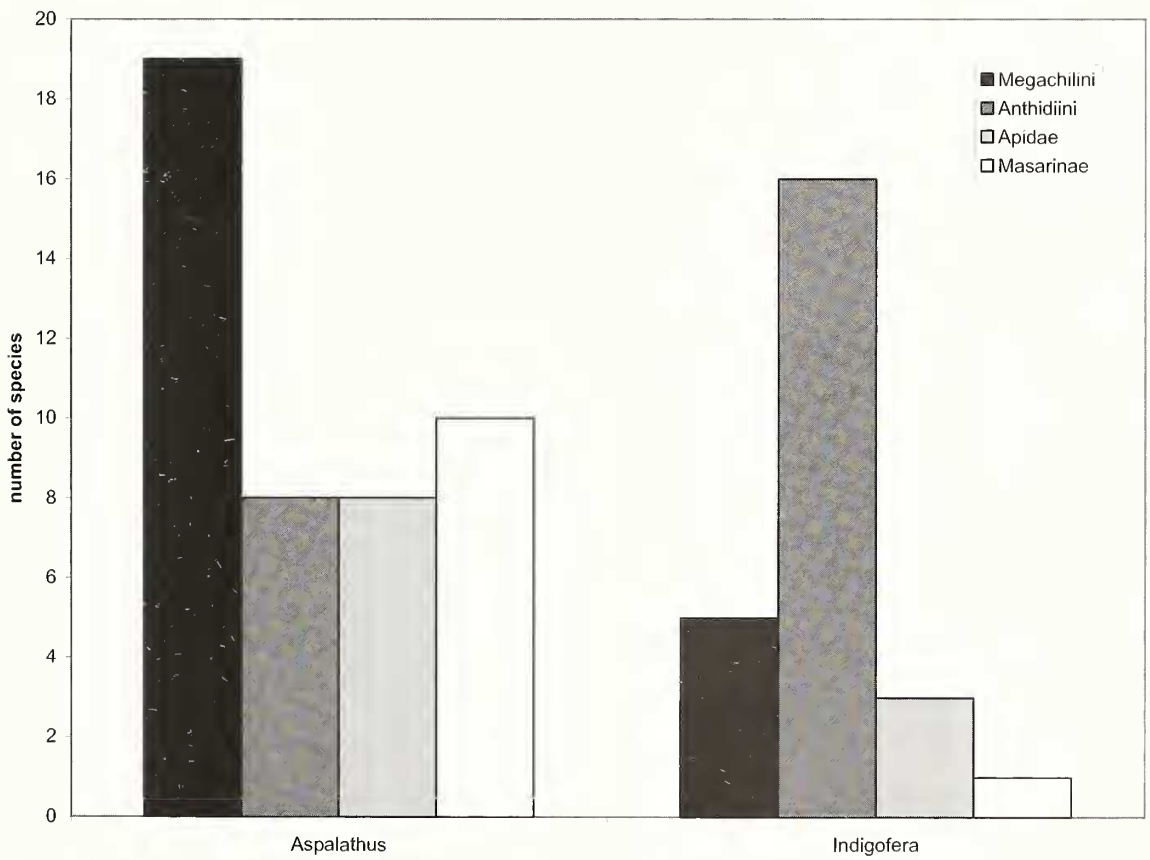

Fig. 20. Comparison of the complexes of bee and pollen wasp visitors to Aspalathus (Papilionoideae: Cape Crotalarieae) and Indigofera (Papilionoideae: Indigofereae)

cyathia, in the Olifants River Valley and Namaqualand. Pompilids were amongst the commonest visitors.

Hemipepsis vindex is an expected visitor to *E. mauritanica*, which in the Gesses' survey was otherwise only recorded as having received a single visit from a male *Chalybion tibiale* (Sphecidae). However, Struck (1994) recorded that *Euphorbia mauritanica* growing in the Goegap Nature Reserve is visited by the bees *Afranthidium (Nigranthidium) cf. concolor* (Megachilidae: Anthidiini), *Scrapter* spp. (as *Polyglossa*) (Colletidae) and *Zonalictus* sp. (Halictidae). For *Euphorbia decussata*, also growing in the Goegap Nature Reserve, Struck recorded visits by bees: *Afranthidium (Branthidium) cf. nitidorubrum* (Anthidiini), *Megachile frontalis* (Megachilini) and *Hylaeus* sp. (Colletidae).

Chamaesyce glanduligera flowers receive a much greater variety of wasp visitors than do *Euphorbia* flowers. In addition to three species of Pompilidae – *Cryptocheilus morosus*, *Psammochares decipiens* and *Schistonyx umbrosus* – it was recorded as being visited by the following wasps: *Parapiagetia subtilis* (Larridae); *Odontosphex damara* (Philanthidae); *Handlirschia scoliaeformis* (Nyssonidae); *Ammophila ferrugineipes* (Sphecidae); *Anthobosca* sp. (Tiphiidae); and *Spintharina arnoldi* (Chrysididae). Only three bees – *Pseudapis cinerea, Pseudapis usakoa* (Halictidae) and *Hylaeus (Deranchylaeus)* (Colletidae) – were, however, recorded. Some of these visitors are widespread, being found from the southeastern Nama Karoo to northern western Namibia. Others have a more northern distribution and yet others appear to be endemic to arid western Namibia. All except *O. damara* were also recorded from flowers of other families.

Southwest of Büllsport, where no other visitors were recorded, *C. glanduligera* was receiving occasional visits from a pollen wasp, *Priscomasaris namibiensis,* which was otherwise abundantly visiting *Limeum sulcatum* (Molluginaceae). This was opportunistic nectar feeding as *P. namibiensis* otherwise favours Aizoaceae: non-Mesembryanthema.

Rosales

Rhamnaceae

The only species of Rhamnaceae sampled was *Ziziphus mucronata*, a shrub or small tree with the greater part of its distribution outside the Karoo Biome to the east and north. It is however present in the extreme southeast and northwest: it was sampled near Adelaide in the southeast over a period of three days during which the flowers were being abundantly visited by wasps. The sample was made up of 13 species of Eumeninae, seven species of Pompilidae, six species of Nyssonidae, four species of Sphecidae and three species of Crabronidae, all polyphagous species. *Ziziphus mucronata* is clearly an important source of nectar for wasps.

EUROSIDS II

Brassicales

Brassicaceae (including Capparaceae)

Brassicaceae is used here in the broad sense (as understood by APG 1998) to include Capparaceae. Three genera were sampled for flower visitors: *Heliophila* in Namaqualand, *Cleome* (Capparaceae) from the northern Richtersveld through the Nama Karoo of Namibia and associated arid savanna and desertic areas, and *Maerua* (Capparaceae) at Vioolsdrif and Rooivaal south of the Orange River.

Herbaceous annual species of *Heliophila* were observed on numerous occasions at various localities, but flower visitors were infrequently recorded. Sampling in the Kamiesberg yielded bees of two families, one each of Megachilidae (Anthidiini) and Colletidae, both polyphagous species. Five species of *Heliophila* were sampled by Struck (1990) in the Goegap Nature Reserve. Collectively they received visits from a single species of Megachilini (Megachilidae), a single species of Anthidiini (Megachilidae), a single species of Colletidae, two species of Anthophorini (solitary Apidae), and *Apis mellifera*, (Apidae).

No records of visits by pollen wasps or wasps were recorded.

Four species of the herbaceous genus *Cleome* were sampled. Yellow-flowered *C. paxii* was sampled in northern Richtersveld, and yellow-flowered *C. angustifolia,* yellow-flowered *C. suffruticosa* and purplish-pink-flowered *C. elegantissima* at numerous sites in Namibia. Collectively, they were visited by 23 species of bees, one species of pollen wasp and one species of wasp. The bee taxa recorded visiting *Cleome* are summarised below:

- Apidae:
  Anthophorini: six species of *Amegilla* and two species of *Anthophora*
  Eucerini: three species of *Tetraloniella*
  Xylocopini: four species of *Xylocopa*
  Apinini: *Apis mellifera*
- Megachilidae:
  Anthidiini: one species of *Eoanthidium*
  Megachilini: four species of *Megachile*
- Halictidae: one species
- Melittidae: one species.

None of the bees listed above is restricted to *Cleome*. However, it is apparent that plants of this genus are particularly attractive to Anthophorini. Additional records for megachilids are those of Whitehead (1984), who collected two species of *Fidelia (Parafidelia)* (Fideliinae) from flowers of *Cleome* in Namibia, and of Struck (1990), who collected two species of Megachilidae from an additional species of *Cleome* in the Goegap Nature Reserve, Namaqualand.

A pollen wasp, *Jugurtia koeroegabensis* and a bee-hunting wasp, *Philanthus triangulum*, were casual visitors, only encountered on *Cleome* at one site (Pootjiespram, in the Richtersveld National Park). In this area *J. koeroegabensis* was more commonly encountered visiting *Peliostomum* (Scrophulariaceae) and *Zygophyllum* (Zygophyllaceae).

Like *Cleome, Maerua schinzii* – a small tree with yellowish white flowers – was favoured principally by polyphagous bees of the families Apidae and Megachilidae and also received casual visits from *Philanthus triangulum*. The bees recorded were *Amegilla niveata* (Anthophorini), *Xylocopa caffra* and *Xylocopa scioensis*

(Xylocopini), *Apis mellifera* (Apini), and *Megachile (Chalicodoma) niveofasciata* (Megachilini). Clearly, other species of Apidae and Megachilidae can be expected.

Malvales

Malvaceae (including Sterculiaceae)

Malvaceae is used here in the broad sense (as understood by APG 1998) to include Malvaceae, Sterculiaceae, Tiliaceae and Bombacaceae. Malvaccae (*sensu stricto*) were not uncommonly encountered in flower but were rarely visited by aculeate Hymenoptera. The purple-violet flowers of *Hibiscus* were occasionally visited by *Tetraloniella cf. michaelseni* (Apidae: Apinae: Eucerini) near Omaruru on the northwestern savanna fringe. The white flowers of a 'mallow' were being visited by *Xylocopa caffra* in the Grootberg Pass west of Kamanjab in the northwest. On a single occasion the pink flowers of another 'mallow' were being visited in large numbers by *Podalonia canescens* (Sphecidae) on the southwest coast. Red, relatively small-flowered *Hibiscus elliottiae* is widespread in the northwest and – as expected from the colour of the flowers – is not visited by aculeates, but by butterflies.

Sterculiaceae is amongst the ten largest families of the Eastern Karoo and the Damaraland-Kaokoveld domains (Cowling & Hilton Taylor 1999).

Fourteen named species of *Hermannia* – representing both subgenera, *Hermannia* and *Mahernia*, and several unnamed species – were sampled across the study area. The flowers of all species are relatively small, downwardly hanging and 'bell-shaped', requiring entry from below.

Overall, 39 species of aculeates were recorded. These included 32 bee taxa: Apidae (including *Apis mellifera*) (13); Megachilidae (15); Melittidae (2); Andrenidae (1), and Halictidae (1). In addition, five pollen wasps and two wasps were taken visiting the flowers of *Hermannia*. The bees all exhibited varying degrees of polyphagy with the possible exception of the two melittids. However, the large diversity of bee visitors was not randomly distributed within the families represented. Of the Apidae, seven were species of Anthophorini (four *Anthophora* – all from the subgenus *Pyganthophora* – and three *Amegilla* of which two were of the previously–recognised subgenus *Zebramegilla*). Of the Megachilidae, nine were Anthidiini.

Visits by pollen wasps – four species of *Jugurtia* and two of *Masarina* – were all from the west, from Ladismith in the south to just south of Opuwa in the north of Namibia. The most widespread species was *Jugurtia confusa*, which has been encountered from northwest of Grahamstown in the southeast to southwest of Windhoek in Namibia. In the Grahamstown district it has been considered to be associated with Mesembryanthema (Gess 1996) but in Namibia was abundantly associated with *Hermannia comosa* at a site east of the Gamsberg Pass. At this site, although a range of other plants were in flower (of which some were visited by other species of *Jugurtia*), none was being visited by *J. confusa* at anytime throughout the day.

Jugurtia alfkeni was encountered abundantly on flowers of two species of *Hermannia* from seven localities in Namibia from Karasburg in the southeast across to the west north of Helmeringhausen and northwards to north of Sesfontein in the Kaokoveld. This species apparently specializes in *Hermannia*, with only three single –probably casual – visits to flowers of other taxa having been recorded.

Jugurtia mandibulata and *J. damara* (Gess 2004) were recorded from *Hermannia* (almost exclusively *H. modesta*) in Namibia, the former from Karasburg north to Palm and the latter from Gross Barmen north to the Kunene. Both of these *Jugurtia* species appear to be specialists.

The association between *Masarina strucki* and *Hermannia*, to which it is apparently restricted, was examined (Gess *et al.* 1997). A nest of this species was investigated and the pollen of the provision found to be solely derived from *Hermannia*. There are no records of visits by this species to flowers of any other plants. *M. strucki* was abundantly encountered on *Hermannia* in Namaqualand, from Springbok south to the Olifants River Valley and from east of the escarpment northeast of Nieuwoudtville, and from the western Little Karoo at Ladismith. Other records of flower visiting for *M. strucki*, made available by Struck and Whitehead, are similarly for *Hermannia* being from the Goegap Nature Reserve and from Ladismith respectively.

The remaining pollen wasp *Masarina mixta* is a casual visitor as it is most commonly associated with *Wahlenbergia* (Campanulaceae).

The two wasps – *Philanthus capensis* (Philanthidae) and *Allocoelia quinquedens* (Chrysididae) – are casual visitors. The presence of *Allocoelia* is, however, of interest as this genus of cuckoo wasp is a 'parasite' solely in the nests of pollen wasps.

In size, behaviour and constancy, the *Jugurtia* and *Masarina* species are suited to be pollinators of the *Hermannia* species which they visit. Indeed, where they occur, they are probably the most reliable potential pollinators. However, in the areas where they are not present, the flowers are adequately serviced by anthophorine and anthidiine bees.

Three species of *Grewia* (Tiliaceae), all shrubs, were observed for flower visitors. The pinkish violet flowered *G. occidentalis* was sampled in the southeastern Nama Karoo northwest of Grahamstown, where it was visited principally by *Xylocopa* spp. (Apidae). In addition, *Xylocopa* was observed visiting the yellow flowers of *G. flava* in the Kalahari and of *G. bicolor* in the Namib. Zietsman (1991) studied the reproductive biology of *G. occidentalis* in the vicinity of Bloemfontein, recording *Apis mellifera* and two species of *Xylocopa* as the only flower visitors. He studied the behaviour of the honeybees and concluded that they are inefficient as pollinators.

It is concluded that *Xylocopa* species can be considered to be the expected visitors to *Grewia*, and although polyphagous and therefore not dependable, to be the most likely pollinators.

A number of other visitors to *Grewia* were recorded in the present study: a single male each of *Tetraloniella apicalis* (Apidae) and *Anthidiellum (Pygnanthidiellum) spilotum* (Megachilidae); a single female *Megachile (Psendomegachile) sinnata latitarsis* (Megachilidae) visiting *G. occidentalis*; and single male nomiines (Halictidae) *Lipotriches (Macronomia)*

sp. and *Nomia (Acunomia) epileuca*, visiting *G. bicolor*. These all appeared to be casual visitors.

Neuradaceae

Neuradaceae is a small family restricted to semi-arid regions. Two genera are represented in southern Africa and a third genus is found in north Africa aeross the Middle East to India. They are prostrate herbs with large, regular, open, yellow flowers. Two species of *Grielum* – *G. grandiflorum* and *G. humifusum* – were sampled at several sites in Namaqualand and in the sandveld to the west of the Olifants River Valley. One species, *Neuradopsis austroafricana*, was sampled in southern Namibia, on the fringe of the Kalahari in the east and on the fringe of the Namib in the west. Visits from 12 speeies of aculeates were recorded. These included: 10 species of bees from five families – Apidae (2), Colletidae (1), Halietidae (2), Megachilidae (4), and Melittidae (1); one species of pollen wasp – a species of *Quartinia* – and one species of wasp – *Stilbum cyanurum* (Chrysididae).

The most commonly encountered visitor to both species of *Grielum* was *Scrapter chloris* (Colletidae), which appears to specialize in flowers of this genus (not having been collected from any other flowers). *G. humifusum* was also frequently visited – in the sandveld but not further inland – by *Fidelia (Parafidelia) hessei* (Megachilidae: Fideliinae), which similarly appears to be a specialist visitor. Visits by other bees were casual and infrequent.

Fidelia (P.) hessei was the most common visitor to *N. austroafricana* on the Kalahari fringe. In this area visits by males of *Meganomia binghami* (Melittidae) were recorded but these were casual in nature as was that of *S. cyanurum*.

It would appear from the above, that *S. chloris* and *F. (P.) hessei* are the most dependable visitors to *Grielum* and *Neuradopsis* and the most likely visitors to be the pollinators.

A pollen wasp, *Quartinia poecila* has, however, since been found to be one of the most abundant visitors to flowers of *Grielum sinuatum* in the southern Namib. It is not, however, restricted to Neuradaceae as it was also visiting Aizoaceae, Asteraceae and Zygophyllaceae.

Myrtales

Combretaceae

Combretaceae are found in most tropical countries and are widespread in southern Africa. They are trees or shrubs. In the present survey only one species, *Terminalia prunioides*, a small tree, was found in full flower and being visited by insects. It was growing to the west of Kamanjab in northwesten Namibia on a stony slope above a dry watercourse. The clusters of small white flowers were being visited abundantly by *Nomia (Acunomia) epileuca* (Halictidae: Nomiinae). This bee, which was encountered throughout the 'karroid' areas of Namibia, is broadly polyphagous, having been recorded from 12 families of plants. It was, however, most widely and frequently recorded from *Tribulus* (Zygophyllaceae). The only other recorded visitor was, rather surprisingly, a single female of *Jugurtia alfkeni*, which shows a marked preference for *Hermannia*. The probable explanation is that herbaceous and small shrubby plants were almost all dried up, with the exception of a labiate from which one female of *N. (A.) epileuca* was taken.

Of significance is the fact that Curtis & Mannheimer (2005) in their comments on 21 species of Combretaceae mention flower visitors for only one species, *T. prunioides* – "bees produce good honey from the nectar".

ASTERIDS

Cornales

Loasaceae

Loasaceae is represented in southern Africa by one species *Kissenia capensis*, occurring in northern Namaqualand and Namibia. In the present survey, flower visits were reeorded for this plant growing in a dry drainage channel in the Namib Desert southwest of Uis. Here the flowers were only receiving visits from males of *Pseudapis usakoa* (Halictidae) and *Pachyanthidium (Ausanthidium) ausense* (Megachilidae: Anthidiini). In the present survey *P. usakoa* was found on flowers throughout Namibia and was recorded from 10 plant families. The anthidiine, *P. (A.) ausense,* was recorded from flowers of five families but most commonly from *Indigofera* (Fabaceae) in the Richtersveld and from *Zygophyllum* (Zygophyllaceae) in Namibia, between Palm and Khorixas.

Struck (1990) sampled *K. capensis* at the southern end of its distribution in the Goegap Nature Reserve. He recorded visits from a female *Amegilla velutina* (Apidae), *Halictus (Seladonia) cf. atroviridis* (Halictidae), and two species of beeflies (Bombyliidae).

Ericales

Ebenaceae

Both genera of Ebenaceae, *Diospyros* and *Euclea* are widely represented in the Karoo, in particular in association with drainage channels. The small greenish or dull cream flowers of these shrubs do not generally attract many wasps and bees.

Euclea crispa was sampled at Karoo Poort at the southern end of the Tankwa Karoo on a day when it was seen to be well attended. The sample was constituted of 11 species of wasps (four species of Philanthidae, two of Pompilidae and one each of Chrysididae, Crabronidae, Eumeninae, Scoliidae and Pompilidae) and two species of bees (one each of Colletidae and Halictidae).

Diospyros was never well attended but was sampled northwest of Grahamstown – where it was visited by *Allodapula* and *Braunsapis* (Apidae: Xylocopinae) – and east of Nieuwoudtville – where its only visitor was the highly polyphagous and widespread eumenine *Delta caffra*. Otherwise, no flower visitors were reeorded.

EUASTERIDS I

Boraginaceae (including Hydrophyllaceae)

Boraginaceae is used here in the broad sense (as understood by APG 1998) to inelude the family

Fig. 3. Nama Karoo, Colesburg

Fig. 4. Eastern extension of Nama Karoo, northwest of Grahamstown.

Fig. 5. Interface between the Succulent Karoo and the Nama Karoo, Prince Albert.

Fig. 6. Western Little Karoo, near Ladismith.

Fig. 7. Dry Fynbos to the west of the Olifants River valley, Clanwilliam Dam in the distance.

Fig. 8. Karroid area in Olifants River Valley, east of Clanwilliam Dam at foot of Cederberg.

Fig. 9. Succulent Karoo, Knersvlakte, Namaqualand.

Fig. 10. Namaqualand Broken Veld, Goegap, Springbok, Namaqualand.

Fig. 11. Succulent Karoo, Koeroegabvlakte, Richtersveld National Park, Namaqualand.

Fig. 12. Southern Namib Desert, south of Rosh Pinah.

Fig. 13. Kalahari fringe, near Köes.

Fig. 14. Interface between Nama Karoo, Succulent Karoo and Desert, northeast of Aus.

Fig. 15. Drainage channel, east of Walvis Bay, Central Namib Desert.

Fig. 16. Drainage channel, north of Cape Cross, Central Namib Desert.

Fig. 17. Nama Karoo, in the vicinity of Khorixas.

Fig. 18. Dry Savanna, west of Gross Barmen.

Hydrophyllaceae. Representatives of six genera were sampled: the woody genus *Ehretia*, and the herbaceous genera *Anchusa, Heliotropium, Lobostemon, Trichodesma,* and *Codon* (Hydrophyllaceae).

All flower-visiting records for Boraginaceae, can be summed up as follows:

- 52 species of bees from five families: Melittidae (5), Andrenidae (2), Halictidae (6), Megachilidae (13), and Apidae (30) (including *Apis mellifera*).
- Five species of pollen wasps.
- Thirteen species of wasps from six families: Scoliidae (3), Nyssonidae (3), Sphecidae (4), Pompilidae (1), Eumeninae (1) and Philanthidae (1).

Blue-flowered *Anchusa capensis*, the only species of this genus represented in southern Africa, was sampled over several years in the southeastern Nama Karoo, at several sites northwest of Grahamstown, at a site near Colesburg, and in Namaqualand at several sites in the Kamiesberg. The bees (from these areas combined) were comprised of the following taxa:

- 18 species of Apidae – Apinae (14) and Xylocopinae (4).
- 10 species of Megachilidae – Anthidiini (3), Megachilini (5), and Osmiini (2).
- Halictidae (1).

Of these, Apinae were the most species numerous and the most often encountered. Of the apines, seven are species of *Anthophora* (four of the subgenus *Heliophila,* two of *Pyganthophora* and one of *Paramegilla*), two are species of *Amegilla*, and four are species of *Thyreus* (cleptoparasites and therefore, like wasps, visiting flowers for adult nourishment only). Of the Xylocopinae two are species of *Allodapula*, one of *Ceratina* and one of *Xylocopa*. No pollen wasps were recorded.

In addition to the bees, 10 species of wasps were taken from *A. capensis* – three species of *Bembix* (Nyssonidae), three species of *Ammophila* and *Podalonia canescens* (Sphecidae), and three species of Scoliidae – all in the category of casual visitors.

Lobostemon is principally a species of the southwestern Western Cape but does extend northwards to Namaqualand and eastwards to the Eastern Cape. Several blue or bluish violet flowered species of *Lobostemon*, including *L. trichotomus* were sampled to the east and west of Clanwilliam. Seven species of Apidae – three Anthophorini (two species of *Anthophora (Pyganthophora)* and *Amegilla niveata*), three Xylocopini (species of *Xylocopa*) and *Apis mellifera*, – were recorded. No other bee families, wasps or pollen wasps were represented.

Two species of *Trichodesma* were sampled. The relatively small purple flowered *Trichodesma cf. africanum* was encountered from northern Richtersveld northwards to the Namib Desert fringe southwest of Uis in northern Namibia in dry drainage channels. The relatively large blue-flowered *Trichodesma angustifolium* was recorded at a site east of the Gamsberg Pass. Both species were visited solely by bees.

Although *T. cf. africanum* was never found to be abundantly visited, the following bees were recorded visiting this species: *Pachymelus peringueyi* (Apidae: Anthophoriniae); *Afranthidium (Immanthidium) junodi* (Megachilidae: Anthidiiini); *Pachyanthidium (Ausanthidium) ausense* (Megachilidae: Anthidiini), and *Pseudapis usakoa* (Halictidae) (which was only recorded at the northernmost site).

Trichodesma angustifolium was visited abundantly, but solely, by four large Anthophorini: three species of *Amegilla – A. nubica, A. atrocincta* and *A. niveata* – and *Anthophora (Paramegilla) basalis*.

White-flowered *Heliotropium ciliatum* is not uncommon on roadsides in Namibia but only once –between Aus and Helmeringhausen in the southwest on the desert fringe – was observed to be receiving visits from aculeates. The only relatively abundant species was a pompilid, *Schistonyx umbrosus*.

Since closing the catalogue for analysis, a second species of white-flowered *Heliotropium, H. tubulosum* (a herb that grows in patches in drainage channels of the Central Namib) was sampled. At several sites it was abundantly visited by two pollen wasps: *Jugurtia namibicola* and a species of *Celonites* (Gess in prep), both of which have been recorded solely from these plants, of which it seems likely that they are pollinators. The forelegs of the *Jugurtia* show similar modifications (Gess 2004) to those of *Trimeria* (Masarinae), which is associated with *Heliotropium* in South America (Neff & Simpson 1985).

The flowers of the violet-flowered shrub, *Ehretia rigida*, are expected to be 'bee flowers'. However, although the flowers were observed on many occasions, only one aculeate visitor – *Celonites capensis*, an unusually polyphagous pollen wasp – was encountered.

Codon – with two species, *C. royenii* and *C. schenkii* – is a southern African endemic. Both species are found most commonly in dry drainage channels in Namaqualand and Namibia. *Codon royenii*, however, is also found in some dry areas further to the southeast. Detailed accounts of the structure of the flower of *C. royenii* and the behaviour of the flower visitors have been given (Gess 1999a; Gess *et al.* 1997). The abundant nectar is not readily accessible, being contained in the base of the relatively large, inverted, bell-shaped flower below tightly adpressed staminal filaments. For nectar to be obtained by a flower visitor, that visitor must be able insert its glossa between the filaments. A pollinator must be large enough so that, when entering a flower to obtain nectar, it comes into contact with ripe anthers or receptive stigmas. The pollinators of both species are considered to be *Xylocopa* species. Both species of *Codon* are, however, also visited occasionally by a very broadly–polyphagous apid, *Amegilla niveata* (Anthophorini), and a megachilid, *Eoanthidium (Clistanthidium) turnericum* (Anthidiini). The most abundant visitors to *C. royenii* in the Richtersveld and the adjoining area north of the Orange River are two species of pollen wasps: *Jugurtia codoni* and an undescribed species of *Quartinia*. In northern Richtersveld, both species were commonly present but *J. codoni* was absent north of the Orange River. The flowers are clearly an important source of both nectar and pollen for

these pollen wasps. Due to their small size and the nature of their behaviour in the flowers, they are not, however, considered to be pollinators. The only wasp visitor to these flowers was *Philanthus triangulum,* a casual visitor.

Vahliaceae

The monogeneric family Vahliaceae is represented in southern Africa by two very variable species, widespread in the drier west. The flowers are small, regular, and open, with free petals. *Vahlia capensis*, a yellow flowered erect herb, was sampled on the banks of drainage channels at Rooibank, on the lower reaches of the Kuiseb River in the Namib Desert, and in the Karas Mountains in southeastern Namibia. At Rooibank the flowers were being visited by an apid, *Amegilla niveata* (Anthophorini), and a megachilid, *Afranthidium (Branthidium) minutulum* (Anthidiini), and in the Karas Mountains by two apids – *Ctenoceratina bilobata* and *Braunsapis otavica /Braunsapis albipennis* (Xylocopini)) – and a megachilid, *Pseudoheriades moricei* (Osmiini). An additional visitor at the site in the Karas Mountains was a pollen wasp, a female *Quartinia propinqua*. This was probably a casual visit as this species was otherwise recorded solely from yellow flowered Asteraceae at sites in the southern great Karoo, Bushmanland and east of the escarpment in Namaqualand.

Gentianales

Apocynaceae

Apocynaceae is used here in the broad sense (as understood by APG 1998) to include the family Asclepiadaceae. The only species of Apocynaceae *(sensu stricto)* visited by aculeates was the shrub *Carissa haematocarpa*, flowering in a dry drainage channel on the Karoo Biome experimental plot on Tierberg Farm, Prince Albert in the southern Great Karoo. Single species of Apidae and Megachilidae were recorded, *Thyreus delumbatus* (Apinae: Melectini) and *Megachile* sp.

Three species of Asclepiadaceae were sampled: *Gomphocarpus filiformis* (syn. *Asclepias buchenaviana*) and *Gomphocarpus sp.*, two non-succulent, perennial, bushy species with heads of relatively small cream flowers; and *Sarcostemma viminale.*, an erect, succulent, perennial species with heads of relatively small yellow flowers.

Gomphocarpus filiformis was sampled on Tierberg Farm, Prince Albert in the southern Great Karoo, in southern Namibia southeast of Karasburg and between Karasburg and Grünau, where it was abundantly visited by diverse polyphagous wasps and bees but not by pollen wasps. The diversity at the southern site was greater than at the northern. This is not surprising as Prince Albert lies in the transition zone between the eastern and western aculeate faunas and also shares some additional species with the northern savanna fauna. The assemblage of visitors to *G. filiformis* includes 42 species of wasps and 27 species of bees.

The wasps represented were as follows: nine species of Pompilidae; seven species of Sphecidae; seven species of Nyssonidae; four species of Tiphiidae; four species of Vespidae (Eumeninae); three species of Philanthidae; three species of Scoliidae; two species of Chrysididae; two species of Crabronidae (Larrinae); one species of Bradynobaenidae.

The bees represented were as follows: 12 species of Megachilidae (Megachilini); two species of Megachilidae (Anthidiini); six species of Apidae (Apinae), including *Apis mellifera*; two species of Apidae (Xylocopinae); three species of Halictidae; one species of Colletidae; one species of Melittidae.

During the present study *G. filiformis* was only once encountered in flower in the northern Namib, namely in a drainage channel near Rössing. At that time it was being visited solely by *Braunsapis otavica/Braunsapis albipennis* (Apidae: Xylocopinae). Nonetheless it is probable that in the Namib Desert there are times when it is, as elsewhere, an important resource for wasps and bees, it having been recorded as a drainage line specialist in the Namib Desert by Jürgens *et al.* (1997).

A second *Asclepias* species was sampled only at Karoo Poort at the southern end of the Tankwa Karoo where it was being visited by three species of Pompilidae and one species each of Apidae, Philanthidae, Sphecidae and Tiphiidae.

Sarcostemma viminale was sampled for the survey at Kommadagga in the southeastern Nama Karoo where the flowers were visited by wasps and bees.

The representation of taxa was as follows:

- Six species of wasps from three families – Nyssonidae (2), Sphecidae (3), and one species of Vespidae (Eumeninae) (1).
- Four species of bees from three families – Apidae (Xylocopinae) (1), Megachilidae (Megachilinae) (2), and (Nomiinae) (1).

Liede & Whitehead (1991) made a study of the pollination biology of *S. viminale*, sampling plants at several sites in Bushmanland and Namaqualand. In addition to wasps and bees they sampled flies, butterflies, moths, beetles and bugs but concluded that it was only the wasps and bees that successfully transferred pollinia and were therefore pollinators of this plant. They listed three species of wasps – one species each of Nyssonidae, Sphecidae and Scoliidae – and three species of bees – one each of Megachilidae (Megachilini), Halictidae (Nomiinae) and *Apis mellifera*. This was a similar complex to that from the southeast.

Many of the aculeates, particularly the wasps, collected from the *Asclepias* species in the present survey bear pollinia and are potentially effective pollinators of these plants.

Lamiales

Acanthaceae

Acanthaceae are listed as one of the ten largest families in the Damaraland-Kaokoveld Domain (Cowling & Hilton Taylor 1999). In the rest of the Karoo-Namib, although not as relatively species-numerous as in the Damaraland-Koakoveld Domain, they are a notable element of the flora. The Acanthaceae found in flower and receiving visits from aculeates were as follows: three species of *Blepharis*, four species of *Monechma*, two species of *Petalidium*, and one species of *Peristrophe*.

Acanthaceae are generally considered to be 'bee

flowers' and the results of the present survey are in line with this thinking. Not only were bees the predominant visitors with respect to number of species (53 species as compared with two species of pollen wasps and 14 species of wasps, taken overall) but also in terms of numbers of individuals visiting the flowers.

Three species of *Blepharis* were sampled. These, together with the sampling areas, are listed below:

- white-flowered *B. capensis* in the southeastern Nama Karoo northwest of Grahamstown and east of Waterford;
- blue-flowered *B. obmitrata* at numerous sites in Namibia, in the northwestern Nama Karoo and the associated dry savanna and desert;
- and yellowish-white flowered *B. inacra*, between Springbok and Kamieskroon in Namaqualand.

The complexes of visitors to *B. capensis* and *B. obmitrata* were very similar. A greater number of species was, however, recorded from the former species than from the latter species. Twelve species of apids (six species of *Amegilla*, two species of *Thyreus* and four species of *Xylocopa*) and nine species of megachilids were collected from flowers of *B. capensis* but only six apids (five species of *Amegilla* and *Anthophora (Pygnanthophora) abrochia)* and two megachilids were collected from flowers of *B. obmitrata*. The species of *Amegilla* were all of the previously recognized subgenus *Zebramegilla*. In addition, *Apis mellifera* were occasionally present on flowers of both species. Halictids of three species were recorded from *B. obmitrata* but none was recorded from *B. capensis*.

Wasp visitors were incidental: four eumenines and a scoliid from *B. capensis* and a nyssonid, *Bembix namibiensis*, from *B. obmitrata*. The only pollen wasp collected from flowers of *Blepharis* was *Ceramius lichtensteinii*, a 'mesem' specialist, which occasionally visits *B. capensis* for nectar.

The four species of *Monechma* sampled, together with the areas in which they were sampled, are listed below:

- pink-flowered *M. mollissimum* in the northern Richtersveld;
- purplish pink-flowered *M. spartioides* in southeastern Namibia;
- purplish pink-flowered *M. divaricatum* in southeastern Namibia;
- violet-flowered *M. genistifolium* in northwestern Namibia.

The *Monechma* species, as a group, were visited by a similar complex of aculeates to that recorded from *Blepharis*: bees of the families Apidae and Megachilidae, and three wasps, which were casual visitors. Ten species of Apidae were recorded: five species of *Amegilla* (two being species of the previously-recognized sub-genus *Zebramegilla*), one each of *Anthophora (Paramegilla), Thyreus* and *Braunsapis,* and two species of *Xylocopa.* Six species of Megachilidae were recorded, including *Megachile (Maximegachile) maxillosa.*

Two species of *Petalidium (P. lanatum* and *P. variabile)* – both associated with drainage channels on the northeastern fringe of the Namib Desert – were sampled. The complex of visitors recorded from these plants differed from those recorded visiting *Blepharis* and *Monechma*. No species of Apidae and only two species of Megachilidae – of the genera *Eoanthidium* and *Coelioxys,* not *Megachile* — were recorded. The only other bee was a halictid, *Pseudapis usakoa*. Two wasps – a sphecid, *Parapsammophila consobrina* and a nyssonine, *Bembecinus* sp. – were recorded from Usakos only. These are considered to be casual visitors.

The only other identified species of Acanthaceae sampled was *Peristrophe cernua* in the southeastern Nama Karoo. This species was visited by three species of bees: two apids – *Amegilla niveata*, which is broadly polylectic, and *Anthophora (Heliophila) vestita*, which shows a strong preference for Asteraceae – and one megachilid, *Megachile (Eutricharaea) stellarum*.

When the catalogue was closed for analysis, no strong sub-generic preference for Acanthaceae by *Anthophora* had emerged. However, recent records from Namibia do suggest that the subgenus *Paramegilla* has a preference for Acanthaceae, comparable to that shown by the subgenus *Heliophila* for Asteraceae and by the subgenus *Pygarthophora* for Zygophyllaceae (Gess & Gess 1996).

Lamiaceae (Labiatae)

Lamiaceae, although not species rich in the Karoo Biome, are present throughout, particularly along drainage channels. Flowers of representatives of nine genera were sampled. These included *Acrotome inflata, Ballota africana, Becium filamentosum, Lasiocorys capensis, Leucas capensis, Leucas pechuelii, Ocimum canum, Stachys aurea, Stachys rugosa* and *Salvia dentata*.

Lamiaceae are generally considered to be bee flowers and the results of the present survey are in line with this thinking. Bees were the predominant visitors with respect to numbers of species and also numbers of individuals. In all, 65 species of bees but only ten species of wasps and two species of pollen wasps were recorded. Representation of bee families was, however, narrow, the following families and species having been recorded:

- Apidae (31), comprised of Apinae (21) and Xylocopinae (10);
- Megachilidae (25), all of which were Megachilinae (Anthidiini (10), Lithurgini (1), Megachilini (8), and Osmiini (6);
- Halictidae (7);
- Andrenidae (2).

Visits by the andrenids *Melitturga* spp., by the pollen wasps and by the wasps (three species of Sphecidae, two species each of Eumeninae and Philanthidae, one species of each of Nyssonidae, Scoliidae, and Chrysididae) were recorded only in the northwest of Namibia on the desert fringe. Visits by the two pollen wasps – *Ceramius damarinus* and *Jugurtia alfkeni* – are of interest, being the only visits by pollen wasps to Lamiaceae recorded in the Afrotropical region, whereas in the Palaearctic, visits to Lamiaceae by some species of pollen wasps are expected (Mauss 1996). The visits by *C. damarinus* and *J. alfkeni* were both opportunistic, having taken place only at one site in a mixed patch of flowers in which their favoured forage plants – *Sesuvium* (Aizoaceae) and *Hermannia* (Sterculiaceae) respectively – were in short supply.

In no part of the study area were Halictidae common visitors to Lamiaceae. The four species were each represented by single records, one from west of the Olifants River Valley in the south, and the other six from three separate sites in the northeast.

The representation of Apinae was as follows:

- the widespread and broadly polyphagous *Amegilla niveata* (from the Western Cape, Namaqualand and northeastern Namibia);
- four other species of *Amegilla* (all of the previously – recognized sub-genus *Zebramegilla*), variously from the southeastern Nama Karoo through the Olifants River Valley and Namaqualand in Succulent Karoo to the northwestern Nama Karoo/Desert fringe;
- two species of *Pachymelus, P. festivus* from the southeast, and *P. peringueyi* from Namaqualand;
- three species of *Anthophora* (all of the sub-genus *Heliophila*) variously from the southwest and Namaqualand;
- four species of *Tetralonia* variously from the Little Karoo to the northeastern fringe of the Namib Desert;
- four species of *Thyreus*, all from the Little Karoo;
- and *Apis mellifera*.

The Xylocopinae were represented by four small carpenter bees, variously from the southwest through to the northwest, and six large carpenter bees (species of *Xylocopa*), variously from the southeast to the southwest and north to Namaqualand.

Megachilini were represented in samples from the extreme southeast, southwest and Namaqualand, but not from north of the Orange River. Osmiini, by contrast, were recorded from Lamiaceae as far north as the northeastern fringe of the Namib Desert, but none was recorded further south than Namaqualand.

Anthidiini were found visiting Lamiaceae only in Namaqualand. The species recorded (variously) from *Ballota africana*, *Stachys aurea* and *Stachys rugosa*.were: three species of *Afranthidium (Immanthidium)*; five species of *Plesianthidium (Spinanthidium)*, and one species of *Pseudoanthidium*.

Pedaliaceae

The Pedaliaceae are principally tropical to sub-tropical and in southern Africa are found mainly in the more northern arid areas. Only one genus, *Sesamum,* was encountered in flower. All plants sampled were erect annual or perennial herbs with numerous large, pink to pinkish-violet gullet flowers. Widespread *S. triphyllum* was sampled from the southern Kalahari north of Upington and in Namibia from the Kalahari fringe in the southeast and along the desert fringe in the west from Helmeringhausen in the south to north of Opuwa in the north. In addition *S. capense* was sampled near Helmeringhausen. Whitehead (1984) and Whitehead *et al.* (1987) sampled two species – *S. rigidum* and an undetermined species – in the Western Cape.

In the present survey, the following visitors to *Sesamum* were recorded: four species of Apidae; three species of Megachilidae; and two species of Halictidae.

Along the desert fringe, from Helmeringhausen/ Spes Bona in the south to Opuwa in the north and in the Kalahari, the large, pink, gullet flowers of *Sesamum* were visited principally by *Fidelia (Parafidelia) friesei* (Megachilidae: Fideliinae). This association supports the records of Whitehead (1987) who, in addition, recorded *F. (P.) ornata* from *S. rigidum.*

The other species of Megachilidae – both species of *Megachile* (Megachilinae: Megachilini) – were generally casual visitors, although *Megachile (Maximegachile) maxillosa* was a not infrequent visitor in southeastern Namibia on the Kalahari fringe.

The most frequently encountered Apidae were species of *Amegilla.* In Namibia these were the widespread and broadly polyphagus *A. niveata, A. langi* and *A. nubica.* In the Western Cape Whitehead (1984) recorded *A. spilostoma.*

There appear to be no bees that are *Sesamum* specialists. However, considering their large size and their behaviour (entering the flowers deeply and moving from plant to plant on a single foraging trip), both *Fidelia (Parafidelia)* and *Amegilla* qualify as potential pollinators.

Scrophulariaceae

Scrophulariaceae is listed as one of the ten largest plant families in all five domains of the Karoo-Namib Region (Cowling & Hilton-Taylor 1999). Following APG 1998, Scrophulariaceae here includes Selaginaceae whereas in Gess (1992) Selaginaceae was treated as a separate family. Of the fourteen tribes (as delimited by Smithies 2000) five – Aptosimeae, Manuleae, Hemimerideae, Cheloneae and Selagineae – were represented in the survey.

As a family, Scrophulariaceae (*sensu lato*) received visits from the sixth largest number of species (98) with little difference in the numbers of species of bees (38), pollen wasps (33) and wasps (27) but marked differences in percentages. The 38 bee species represent only 8.98% of the total number of bee species recorded from all plant families in the entire survey and the 27 wasp species only 7.2% of the wasp species but the 33 pollen wasp species represent 25.58% of the total number of pollen wasps recorded. All of the bee families, but only half of the wasp families, were represented.

Of the bees, 38 species from six families were recorded: Halictidae (15); Apidae (12); Colletidae (4), Megachilidae (4); Melittidae (2), and Andrenidae (1).

Of the wasps, 27 species from seven families were recorded: Chrysididae (3); Vespidae (Eumeninae) (1); Nyssonidae (5); Philanthidae (2); Pompilidae (3); Sphecidae (7); Tiphiidae (6).

Taking the tribes of Scrophulariaceae separately, expected striking differences linked to flower form and presentation are apparent.

Selago (Selagineae) is principally southern African in distribution, widespread but mostly in the Western and Eastern Cape (Smithies 2000). Four species were sampled: *S. corymbosa* in the east, northwest of Grahamstown; *S. minutissima* and *S. verna* in Namaqualand, in the Kamiesberg, and in the vicinity of Springbok; and *S. dinteri* in western Namibia to the east of the Gamsberg Pass.The small, erect, nectar-producing, tubular flowers, aggregated

into corymbs or elongated panicles, are attractive to a diverse range of bees and wasps. In addition, two species of pollen wasps – *Jugurtia braunsi* at the Namaqualand sites and *Ceramius damarinus* in Namibia – have been recorded visiting *Selago*, but only as a secondary resource.

The Manuleae found to be attractive to aculeates all have small, tubular, nectar-producing flowers. The following species were sampled: *Phyllopodium cuneifolium* in the southeast; *Polycarena* species in Namaqualand and to the west of the Olifants River Valley, and *Jamesbrittenia canescens* in Namibia. The most commonly encountered visitors to violet flowered *P. cuneifolium* were species of Ammophilinae (Sphecidae), which were nesting nearby. Other wasp visitors recorded were nyssonids and a pompilid. In addition, visits by two bee species – an allodapine and a halictine – and by one pollen wasp, *Celonites capensis*, were recorded. The two bees visit a wide range of flowers and *C. capensis* is one of the most polyphagous species of pollen wasps, having been recorded from flowers of seven families. The *Polycarena* species, all white flowered, were visited as a secondary resource by pollen wasps.

Yellow-flowered *J. canescens* was observed for visitors near Mariental and between Büllsport and Sesriem. At both sites the visitors were polyphagous bees, principally species of *Amegilla* (Apidae: Apinae: Anthophorini) with (in addition at the second site) *Serapista rufipes* (Megachilidae: Megachilinae: Anthidiini). By contrast, dark red flowered *J. canescens* observed for flower visitors in the Kamiesberge were predictably ignored by the abundant aculeates visiting other plants in flower, but were being visited by butterflies.

Oftia africana – observed near Graafwater, to the west of Clanwilliam – was visited by *Anthophora (Heliophila) wartmanni* (Anthophorini). This bee most commonly visits Asteraceae and, less commonly, a wide range of flowers.

Of the Hemimerideae, two genera were represented: *Nemesia* and *Diascia*. For *Nemesia*, only one visit on one occasion was recorded: that of a single female *Ceratina* (Apidae: Xylocopinae: Ceratini) visiting *Nemesia cf. bicornis* at Wallekraal southwest of Springbok. The spurred, oil-producing *Diascia* flowers and the co-evolved bees of the genus *Rediviva* (Melittidae) – with front legs suited to fitting the spurs and to collecting oil – have been the subject of special study (Steiner & Whitehead 1990; Whitehead & Steiner 2001). In the present survey, two species of *Rediviva* were observed visiting *Diascia*. The associations of bee to flower were, as was expected: *R. longimanus* to *D. longicornis* and *R. emdeorum* to *D. namaquensis*. In addition, flowers of both species were being visited by an opportunist bee, *Lasioglossum* sp. (Halictidae).

The Aptosimeae are – as their common name, Karoo violets, indicates – a feature of karroid areas. One of the three genera, *Aptosimum*, is widespread throughout the karroid and savanna areas of southern Africa, but is most species diverse in the karroid areas. *Peliostomum* is less widespread and *Anticharis* is solely desertic but not restricted to southern Africa, being also found in the Arabian Peninsula and India. The flowers are bluish-violet to purplish, nectar-producing, gullet flowers. Detailed accounts of the structure of the flowers of *Aptosimum* and *Peliostomum*, and of the behaviour of visitors to the flowers and their potential as pollinators, are given in Gess (1996, 2000). The corolla is tubular over the greater part of its length, and very narrow in the basal region, protecting the nectaries from all but long-tongued or minute visitors. There are four stamens in two pairs: a pair with relatively long filaments and a pair with relatively short filaments. In *Aptosimum* the shorter pair of stamens is sterile. The anthers are adpressed in pairs and positioned dorsally in the flower. The style is situated in the dorsal groove. In the freshly opened flower the stigma barely projects at the mouth of the corolla but, with time, the style elongates and curves downward.

Fourteen species of Aptosimeae – eight species of *Aptosimum*, three species of *Peliostomum* and three species of *Anticharis* – were observed for flower visitors. Throughout their range Aptosimeae were visited predominantly by pollen wasps. Twenty two species were involved. Of these, specialist *Celonites* species are considered to be the most important pollinators (Gess 1996, 2000; Gess & Gess 1989; Gess *et al.* 1997). The *Quartinia* species, with one possible exception, are not specialist visitors and are generally – except where the flowers are undersized – too small to be pollinators (Gess 1996). The highest number of masarine genera and species visiting Aptosimeae has been recorded from the northern Richtersveld where, in addition to two species each of *Celonites* and *Quartinia*, one species each of *Jugurtia* and *Masarina* are amongst the visitors.

Visits from bees are very uncommon in the south but in Namibia and the Kalahari to the north of the Orange River, visits from bees are sufficiently frequent to be expected. Sixteen species of bees were recorded, most being uncommon casual visitors. Some were, however, encountered at several sites: *Meliturgula haematospila* (Andrenidae: Panurginae), and *Nomia (Acunomia) epileuca* and *Pseudapis cinerea* (both Halictidae: Nomiinae). Unlike the pollen wasps – all of which have long tongues suited to reaching the nectar at the base of the narrow tube – none of the bees is equipped to reach the nectar at the base of the corolla tube. *Meliturgula haematospila* is a small, flattened bee, which would not activate the release of pollen. It is possible that the nomiines might, in forcing themselves into the flowers, do so. All the bees are polyphagous, *M. haematospila* having been recorded from nine flower families and the two nomiines, *N. (A.) epileuca* and *P. cinerea*, from 14 and 12 families, respectively.

Apart from a single casual visit by a species of *Meria* (Tiphiidae) to *Aptosimum procumbens* in the southeast, no wasp visits to Aptosimeae were recorded.

Solanales

Solanaceae

Solanaceae are widespread in the Karoo Biome but are not highly species diverse. *Lycium, Solanum* and *Nicotiana* were observed for flower visitors. Overall, 11 species of bees and eight species of wasps (but no pollen wasps) were recorded. The flowers of all the species of Solanaceae sampled were visited by bees of the family Apidae, all by species of *Xylocopa*. Flowers of *Lycium* were also visited by three species of Anthophorini and one species of Eucerini. Less commonly, *Lycium* and *Solanum* were

visited by Halictidae. Only *Lycium* was visited by wasps: four species of Eumeninae; two species of *Ammophila* (Sphecidae: Ammophilinae); *Sphex decipiens* (Sphecidae: Sphecinae); and *Campsomeriella (Campsomeriella) caelebs* (Scoliidae).

Generally, relatively large bees are required to pollinate Solanaceae, particularly those species with anthers that require to be "buzzed" in order to release pollen. However, observations suggest that wasps may be contributory pollinators of *Lycium,* which provides easily accessible nectar.

EUASTERIDS II

Apiales

Apiaceae (Umbelliferae)

Apiaceae are not species diverse in the Karoo Biome but, where they occur, some species form large stands. Two indigenous species were sampled: *Berula erecta* in the southeast, and *Deverra denudata* in drainage channels in the southern Kalahari, western Richtersveld and the Namib fringe north of Aus. One exotic species was also sampled: *Foeniculum vulgare,* a common roadside weed in the southeast. All three of the above-mentioned species have small, simple, shallow, nectar producing, yellow flowers massed in umbels.

Apiaceae, represented by these three species, was the family receiving the fourth highest number of flower visitors. However, whereas the three families (Asteraceae, Fabaceae and Aizoaceae) that receive larger numbers of visitors, are widespread and were widely sampled, Apiaceae were limited to a small number of sites. Of all families sampled, Apiaceae received visits from the highest percentage (42.93%) of wasp species.

Of the wasps, 161 species from 13 families were represented: Chrysididae (13); Bradynobaenidae (2); Mutillidae (1); Pompilidae (31); Scoliidae (12); Tiphiidae (8); Vespidae (Eumeninae) (15); Astatidae (1); Crabronidae (27); Nyssonidae (21); Pemphredonidae (2); Philanthidae (16); and Sphecidae (12).

By comparison, the percentage (6.38%) of bee species was small. In all, 27 species of bees from four families were recorded: Apidae (8); Colletidae (6); Halictidae (9); and Megachilidae (4).

No pollen wasps were recorded.

Visitation of these plants by such a wide range of aculeate visitors of suitable size and behaviour is likely to ensure pollination, particularly where – as is usually the case – Apiaceae form considerable monospecific stands.

Asterales

Asteraceae (Compositae)

Asteraceae is the largest family in the Karoo-Namib Region and the largest in four of the five domains listed by Cowling & Hilton-Taylor (1999), being exceeded only in the Namaqualand-Namib Domain by Aizoaceae. Not only are Asteraceae notable for their species diversity but they are also amongst the dominant plants in most karroid areas.

Asteraceae were sampled throughout the study area. All six tribes characteristic of the semi-arid to arid areas of southern Africa were represented. Woody, shrubby species and annual and perennial herbs are included. The flower heads are simple or compound, loose or compact, deep or shallow, with or without ligulate florets.The number of species of Asteraceae sampled was in excess of 75. In total they were recorded as receiving visits from 329 species, species of bees, pollen wasps and wasps combined – i.e. 35.49% of the 927 species visiting flowers. This is the largest number of species recorded from a single plant family. This complex was constituted of 157 species of bees, 56 species of pollen wasps and 116 species of wasps.

The bees visiting flowers of Asteraceae represented all bee families. Of all bee species collected from flowers in the survey 37.12% were represented. The complex was constituted of 157 species in six families: Andrenidae (1); Apidae (51); Colletidae (19); Halictidae (29); Megachilidae (53); and Melittidae (4). Most of these species are broadly polyphagous, however, some specializations are apparent. At least seven species of *Scrapter* (Colletidae) and *Fidelia braunsiana* (Fideliinae) show a marked preference for Asteraceae, having been collected from flowers of this family only. Furthermore, if numbers of recorded visits by species to Asteraceae are compared with numbers of visits by the same species to plants of other families, additional taxa showing preferences can be recognized. Examples are as follows: some species of three genera of Halictidae, *Halictus, Lasioglossum* and possibly *Patellapis*; many of the Osminini (Megachilidae); and some of the Apidae, especially *Anthophora (Heliophila)*, which shows a strong preference for Asteraceae (Gess & Gess 1996).

Of the species of pollen wasps collected on flowers, 43.41% visit Asteraceae, this being second only to Aizoaceae from which 46.51% were taken. Of the 56 species that visit flowers of Asteraceae, 21 species (i.e. seven species of *Ceramius*, three species of *Jugurtia*, and *circa* 11 species of *Quartinia*) specialize in visiting these flowers. The remaining species visit a limited range of other families. Certainly in areas where pollen wasps specializing in Asteraceae are common, they are probably important potential pollinators of the plants that they visit and, in some areas, are probably the most important potential pollinators.

Amongst the wasp species collected on flowers, 30.93% visit Asteraceae. Ten families, comprising 116 species, are represented: Chrysididae (18); Crabronidae (18); Vespidae (Eumeninae) (14); Nyssonidae (21); Pemphredonidae (1); Philanthidae (9); Pompilidae (7); Scoliidae (8); Sphecidae (12); and Tiphiidae (8). Most species are broadly polyphagous. Exceptions are some species of Chrysididae – most notably three species of *Allocoelia* that were repeatedly collected solely on Asteraceae – and some Eumeninae, most notably species of *Raphiglossa.*

Some species of Asteraceae are widely distributed and are common to a range of vegetation and soil types. Whereas some of the aculeate visitors are similarly able to make a living in such diverse situations, most are more restricted in their distributions and their habitat requirements. This results in different complexes of visitors being present at different sites. For example, *Athanasia trifurcata* (Anthemideae) at some sites is principally visited by

pollen wasps, the species varying between sites: *Ceramius braunsi* to the south of Clanwilliam; *Ceramius metanotalis* to the north of Clanwilliam; and *Ceramius toriger* in the southern Tankwa Karoo. At other sites no pollen wasps are present and *A. trifurcata* is principally visited by a diverse complex of wasps and bees.

Similarly, *Berkheya fruticosa* (Arctoteae) is visited by *Ceramius braunsi* at Clanwilliam, by *Ceramius nigripennis* in Namaqualand, and by *Ceramius toriger* to the east of Nieuwoudtville. At most sites bees were uncommon visitors; however, in the Nieuwoudtville area a wide range of bees is represented in the samples.

Vogel (1954) considers that South African composites are generally 'Hymenoptera-flowers', although flies and certain beetles may also play a large part in the pollination of some species. The suitability of most Asteraceae as a floral resource for aculeates and the suitability of aculeates as pollinators has been discussed by Gess (1996). The authors' observations of beetles and flies as visitors suggest that, generally, beetles are destructive visitors but some do exhibit the requirements for pollinators. Flies are generally of less importance than aculeates but in some instances are specialist pollinators. Examples of probable beetle and fly pollination are given by Picker & Midgely (1996) and Johnson & Midgely (1996) respectively.

Campanulaceae

The family Campanulaceae is mainly temperate and sub-tropical in distribution. Although cosmopolitan the family is best represented in the Mediterranean and southern Africa. There are two well-marked subfamilies: the Campanuloideae, with regular flowers and anthers free; and the Lobelioideae, with highly irregular, resupinate flowers and connate anthers. These two sub families are connected by a small group of transitional genera that are sometimes treated as a third sub family, the Cyphioideae.

Visits to flowers of Campanulaceae were recorded for 33 species of bees (7.80% of the species of bees recorded from flowers), 19 species of pollen wasps (14.73% of the species of pollen wasps recorded from flowers) and only nine species of wasps (2.4% of the species of wasps recorded from flowers).

CAMPANULOIDEAE

The majority of records were for Campanuloideae, represented by two genera *Wahlenbergia* (including *Lightfootia*) (13 identified species and several additional species) and *Microcodon* (one species), all from south of the Orange River. The majority of species (11) were from the west, and three species were from the east. The flowers of nine of these species – all from the west – are deeply campanulate, and the flowers of the other five species are shallowly campanulate to stellate. The flowers of most species are violet (bluish to purplish); however, those of one species are white, those of another pink and, of a third, yellow. The structure and pollination strategies of ten species showing various flower forms and the potential of the visitors – based on size and behaviour – to be successful pollinators of the flowers have been investigated in considerable detail (Gess 1996, 1999b; Gess & Gess 1989).

Together, the species of Campanuloideae received visits from 30 species of bees, 16 species of pollen wasps, and four species of wasps. Thirty bee species from five families were represented: Apidae (10); Melittidae (7); Megachilidae (6); Halictidae (5); and Colletidae (2). In the west the visits of all groups, except pollen wasps and melittid bees, were infrequent and casual.

Beeflies and butterflies on occasion visit the deeply campanulate flowers for nectar but are not pollinators. Pollen wasps were the most numerous and reliable visitors to the deeply campanulate flowers and amongst these are several specialist *Celonites*, which are dependable pollinators. Melittid bees are amongst the less frequent visitors. Melittid bees, on the other hand, were the most numerous and reliable visitors to the stellate flowers. Amongst these are specialists: two undescribed species of *Hesperapis*, which are dependable pollinators of these flowers. Pollen wasps are less frequent visitors to these flowers and, even when numerous, are unlikely to pollinate them.

Wahlenbergia flowers sampled in the southeast are shallowly campanulate to stellate. Melittid bees are not available as pollinators as they do not occur in the east and no pollen wasps have been recorded from them. The candidates for pollinators are polyphagous bees. *Ceratina (Ctenoceratina) armata* (Apidae: Xylocopinae: Ceratinini) was the most frequently collected species during two summers of sampling. Two megachilids – *Megachile (Eutricharaea) semiflava* (Megachilini) and *Afranthidium (Branthidium) guillarmodi* (Anthidiini) – were less frequently collected, and a colletid, *Colletes fascicularis,* was collected only once.

CYPHIOIDEAE

Only one record was obtained for Cyphioideae –represented by the single genus *Cyphia*. This was for a male of one polyphagous species, *Amegilla spilostoma* (Apidae: Apinae: Anthophorini), collected from *Cyphia* in the southeast.

LOBELIOIDEAE

Records were obtained for only two species of Lobelioideae: dark-bluish-purple-flowered *Lobelia linearis*, and purple-flowered *Monopsis debilis*. The visitors to *L. linearis*, growing near Nieuwoudtville, were two similarly-sized species: a small, relatively polyphagous carpenter bee, *Ceratina (Ctenoceratina) armata,* and a pollen wasp, *Celonites lobeliae*. Both are suited to pollinating the flowers. It is of interest that small carpenter bees have occasionally been observed visiting *Lobelia* in the southeast.

Monopsis debilis forms dense patches in moist areas from Namaqualand south and west of Clanwilliam. The flowers – as is the case for many dark purple flowers – appear to attract few insects, although they are striking to the human eye. These flowers are visited abundantly, however, by a single species of bee, *Haplomelitta ogilviei* (Melittidae: Dasypodainae: Sambini). In the present survey 67 voucher specimens, including both females and males, were taken and visits by many more individuals were observed at various sites in Namaqualand, the Olifants River Valley and to the west. Furthermore, Rozen (1974)

– when investigating the nesting biology of *H. ogilviei* at Velddrif to the southwest of Citrusdal – found *M. debilis* to be the source of most of the provisions. No other visitors have been recorded. Whether or not *H. ogilviei* extends throughout the range of *M. debilis* remains to be determined, but it is certainly known from the greater part of its distribution. The evidence so far assembled suggests a mutualistic dependence between *M. debilis* and *H. ogilviei,* the latter being apparently the sole pollinator of *M. debilis* in the areas investigated and *M. debilis* being apparently the principal source of provision of *H. ogilviei* (Gess & Gess 1994b).

Haplomelitta ogilviei is not entirely restricted to *M. debilis*, having been occasionally recorded from Asteraceae and *Wahlenbergia* in the present study and from Asteraceae by Rozen (1974). However, these plants are considered to be minor, secondary resources.

DISCUSSION

In the survey of flower visiting in the semi-arid to arid areas of South Africa flowers of 36 families of plants, represented by c 600 species, were recorded as visited by bees and/or aculeate wasps (divided into wasps and pollen wasps). Of these plant families, 34 received visits from bees, 29 from wasps and 21 from pollen wasps. In total, the number of species of bees, pollen wasps and wasps recorded from flowers was 924 (420 species of bees, 129 species of pollen wasps and 375 species of wasps). Calculation of diversity of choice at the specific level demonstrated that bees (taken as a group) and wasps (taken as a group) show similarly high diversity of choice at the specific level. Calculation of diversity of choice at the specific level for each bee family, however, shows that two families of bees – Melittidae and Colletidae –show a relatively low diversity of choice similar to that of pollen wasps. This suggests a lower degree of polyphagy and a higher degree of oligophagy in these three taxa as compared with the other bee families and the wasps.

At the times when sampling of flowers took place, few monocots were attracting visits from bees, wasps or pollen wasps. Nonetheless the recorded visits taken together with published records demonstrate striking differences between families. Asparagaceae – with small, open, shallow flowers offering small quantities of nectar – attract visits from wasps but no bees or pollen wasps whereas Asphodelaceae and Iridaceae – both including species with larger, more complex, deeper flowers, offering larger volumes of nectar per flower – attracted visits from bees and/or pollen wasps but no wasps.

Of the 36 plant families visited the majority (33) were Dicots. The six families attracting visits from the highest numbers of species were Asteraceae, Fabaceae, Aizoaceae, Apiaceae, Zygophyllaceae and Scrophulariaceae (Table 1 and Figure 21). The numbers of species of visitors to these plant families recorded were 329, 320, 224, 198,136 and 98 respectively. The numbers of recorded species of visitors to the other families ranged down from 79 to one. Numbers of visitor species present at sampling sites and the number of plant species sampled might be considered to be a factor in the cases of the first three families (Asteraceae, Fabaceae and Aizocaceae) for which 82, 60 and 79 species, respectively, were sampled at a wide range of sites This cannot, however, be considered to be the full explanation when it is noted that for Apiaciae and Zygophyllaceae only four and 13 species, respectively, were sampled. Furthermore, for example, Apocynaceae (of which only four species were sampled) received visits from 69 species, whereas Malvaceae (of which 21 species were sampled) received visits from a comparable 67 species.

Many differences in relative proportions of wasp, pollen wasp and bee visitors between families are striking (Table 1). Visitor complexes to the six families attracting visits from the highest number of species are compared in Figure 21. Such differences can be linked to flower structure and nectar yield. For example, Apiaceae, which have small, shallow flowers yielding small quantities of nectar attracted visits from 161 wasp species but only 27 bee species. Lamiaceae – which have larger, deep gullet flowers yielding larger quantities of nectar concealed in the bottom of a corolla tube – attracted visits from only 10 wasp species but 65 bee species. No species of pollen wasps were recorded visiting Apiaceae, but two species were recorded from Lamiaceae.

For some families, for which the differences in the proportions of bees to wasps overall are not marked, striking differences are apparent at sub family level. For example, in the Fabaceae the differences in numbers of wasps (147 species) and bees (164 species) are not marked, however, for the sub-families there are marked differences (Figure 19). The differences in the proportions of wasps to bees visiting these sub-families can be related to flower structure and mode of presentation of nectar.

Furthermore, within the Papilionoideae, differences are of note, as illustrated by comparing complexes of visitors to Cape Crotalarieae as represented by *Aspalathus* and Indigofereae as represented by *Indigofera*. Cape Crotalarieae are the only Papilionoideae which recieve regular visits from pollen wasps, most of which are specialist species. However, whereas the complexes of bees (all polyphagous) visiting Cape Crotalarieae, are constituted of similar taxa throughout the range of these plants, the pollen wasps are restricted to the southwest.

Visitors to Aizoaceae and Asteraceae are constituted of relatively high numbers of wasps, pollen wasps and bees – Aizoaceae receiving visits from 76 species of wasps, 98 species of bees, 60 species of pollen wasps and 98 species of bees, respectively, and Asteraceae from 116 species of wasps, 157 species of bees, 56 species of pollen wasps and 157 species of bees respectively. The numbers for pollen wasps are higher than for any other family and the degree of oligophagy is high. Amongst the bees are highly polyphagous species but also species that show strong preferences for Aizoaceae or for Asteraceae. Differences in composition of visitor complexes are distinguishable between subtaxa and between geographic areas. Such differences are also striking within the Zygophyllaceae in which *Zygophyllum* species in the southwest are visited solely by bees, whereas further north they are visited, in addition, by pollen wasps for which they provide an important resource. In the north some species are visited by a considerable diversity of wasps for which they are an

important source of nectar in the arid areas.

Close associations between flowers and visitors are particularly marked in some plant genera or species with restricted access to nectar and/or pollen. Amongst the few visitors to *Aptosimum, Peliostomum* and *Anticharis* (Scrophulariaceae) are pollen wasps of the genus *Celonites*, various species of which are restricted to these flowers and are their most dependable pollinators from the extreme southeast to the extreme north of the study area. Within the genus *Wahlenbergia* (Campanulaceae), species can be grouped according to three flower forms. The visitors to each differ and those that are the most dependable pollinators are species which specialize in visiting the flowers. In the south west one form is suited to a limited number of melittid bees, the second to pollen wasps and the third to monkey beetles. In the southeast, however, none of these taxa were recorded from *Wahlenbergia* which in that area was visited by a small xylocopine, a colletid and a megachiline.

Flowers that attract a single species of visitor are exceptional. For example, the flowers of *Monopsis debilis* – at all sites where they were sampled –attracted only a single species of melittid, *Haplomelitta ogilviei*, which appears to be their sole visitor and sole pollinator. *Haplomelitta ogilviei*, however, is not entirely monophagous as it does visit some other flowers to obtain nectar. Another example of flowers that appear to attract a single visitor are those of *Tylecodon hallii* which is visited by a single species of pollen wasp, *Masarina tylecodoni*, which appears to be monophagous. Furthermore both the plant and the insect are narrowly endemic, both having been recorded only from northern Richtersveld and in a very small area across the Orange River.

CONCLUSIONS

Although a relatively small number of the plant species of the entire study area has been sampled, the survey (as synthesized above) has provided sufficient evidence to draw a number of conclusions, as outlined below.

- The flowers of some plants attract a very large range of aculeates, bees, wasps and in some cases pollen wasps; however, there are no flowers that are attractive to all the available aculeates at any one site.
- The flowers of some taxa of plants are primarily attractive to bees, others to wasps and yet others to pollen wasps.
- The flowers of plants of some subfamilies, tribes or genera attract recognizable, consistently-constituted, complexes of a limited number of aculeate

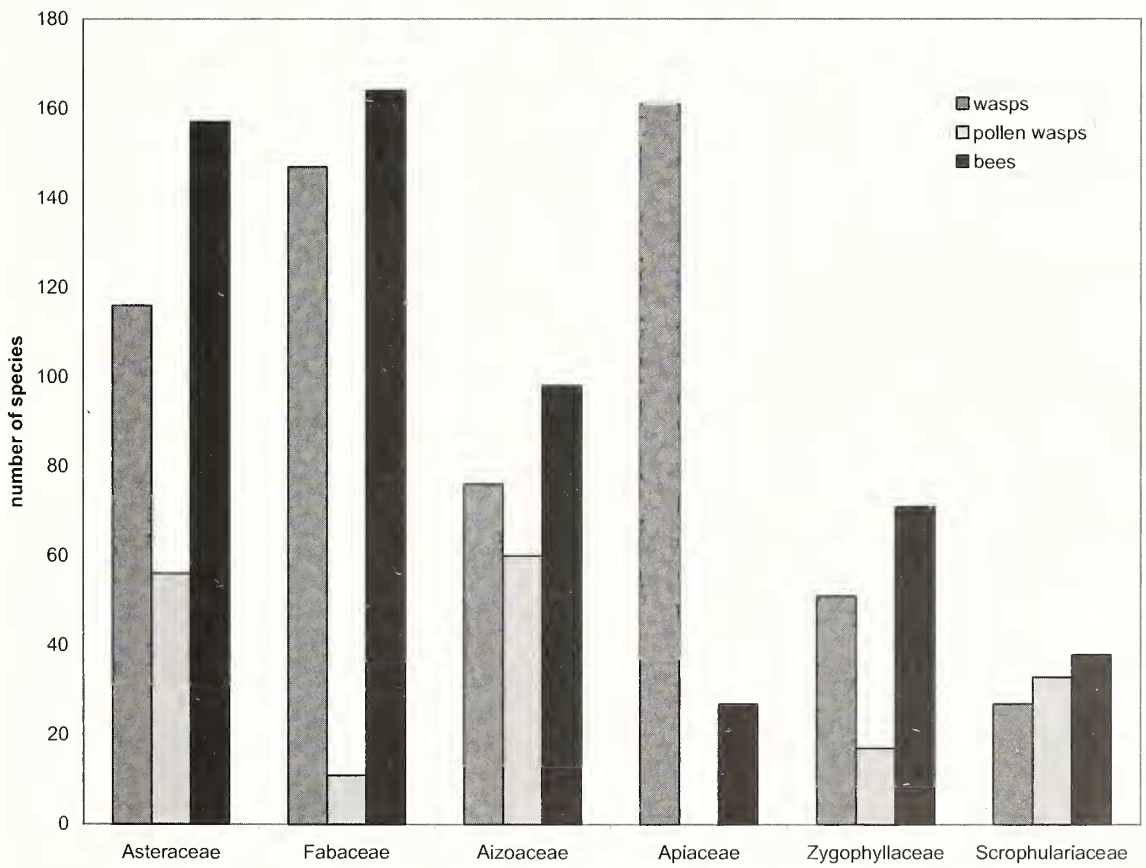

Fig. 21. Comparison of the complexes of wasp, pollen wasp and bee visitors to the six families receiving visits from the largest numbers of species.

taxa throughout the study area.
- The flowers of some taxa show marked differenees in attraction along east/west, south/north gradients.
- The flowers of most plants are pollinated by a complex of bee visitors, which vary from broadly polyphagous through narrowly polyphagous to oligophagous and from widely distributed to narrowly endemic.
- Fewer flowers are visited by pollen wasps but most of these are pollinated by their pollen wasp visitors which vary from narrowly polyphagous to more commonly oligophagous, and from widely distributed to narrowly endemic.
- Flowers visited, and pollinated by, wasps are mostly small open flowers, but some specialist flowers – such as species of Apocynaceae (formerly Asclepiadaceae) – are pollinated by wasps.
- The flowers of some plants attract a single species of aculeate that pollinates the flowers; this is exceptional.

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APPENDICES

APPENDIX 1: Classification of aculeate wasps and bees used in the present work – follows that used by Goulet & Huber (1993), and of bees below superfamily level that of Michener (2000). (Only taxa occurring in Southern Africa are listed).

HYMENOPTERA: ACULEATA
Superfamily Chrysidoidea
- Family Bethylidae (no records)
- Family Chrysididae
  - Subfamily Amiseginae (no records)
  - Subfamily Chrysidinae
    - Tribe Allocoeliini
    - Tribe Chrysidini
    - Tribe Elampini
    - Tribe Parnopini
- Family Dryinidae (no records)

Superfamily Vespoidea
- Family Tiphiidae
  - Subfamily Anthoboscinae
  - Subfamily Myzininae
  - Subfamily Methocinae (no records)
  - Subfamily Tiphiinae
- Family Sapygidae (no records)
- Family Mutillidae
  - Subfamily Sphaeropthalminae
    - Tribe Dasylabrini
  - Subfamily Mutillinae
    - Tribe Mutillini

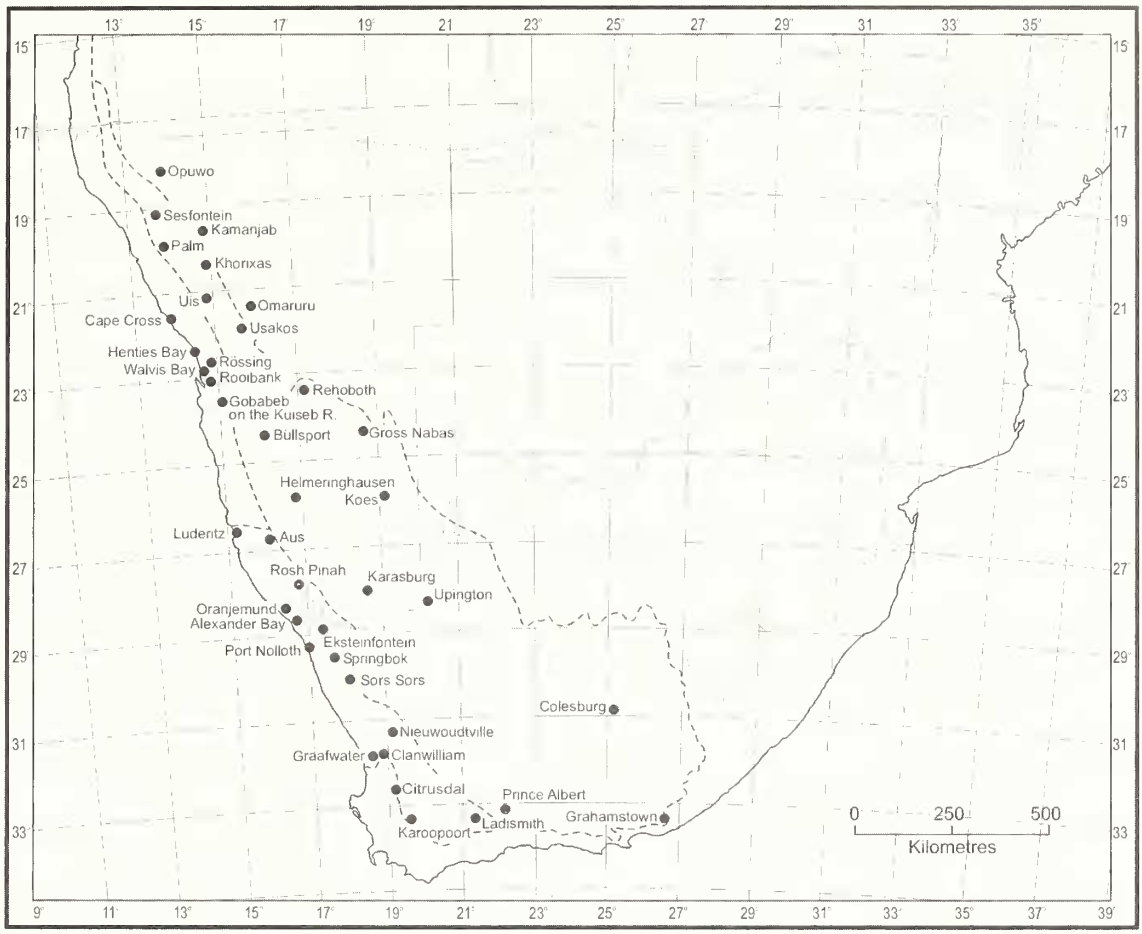
(no records for other subfamilies)
- Family Pompilidae
  - Subfamily Pepsinae
    - Tribe Pepsini
    - Tribe Auplopodini
  - Subfamily Pompilinae
    - Tribe Aporini
    - Tribe Pompilini
  - Subfamily Ceropalinae (no records)
- Family Rhopalosomatidae (no records)
- Family Bradynobaenidae
  - Subfamily Apterogyninae
- Family Scoliidae
  - Subfamily Campsomerinae
  - Subfamily Scoliinae
- Family Vespidae
  - Subfamily Masarinae
    - Tribe Masarini
      - Subtribe Priscomasarina
      - Subtribe Masarina
  - Subfamily Eumeninae
  - Subfamily Polistinae (records not included))
- Family Formicidae (records not included)

Superfamily Apoidea

Apoidea: Spheciformes
- Family Ampulicidae
  - Subfamily Dolicurinae (no records)
  - Subfamily Ampulicinae
- Family Sphecidae
  - Subfamily Sceliphroninae
  - Subfamily Sphecinae
  - Subfamily Ammophilinae
- Family Pemphredonidae
  - Subfamily Pseninae
  - Subfamily Pemphredoninae
- Family Astatidae
  - Subfamily Astatinae
- Family Crabronidae
  - Subfamily Crabroninae
  - Subfamily Larrinae
- Family Nyssonidae
  - Subfamily Alyssoninae (no records)
  - Subfamily Nyssoninae
  - Subfamily Gorytinae
  - Subfamily Stizinae
  - Subfamily Bembicinae
- Family Philanthidae
  - Subfamily Odontosphecinae
  - Subfamily Philanthinae
  - Subfamily Cercerinae

Apoidea: Apiformes
- Family Colletidae
  - Subfamily Colletinae
  - Subfamily Hylaeinae
- Family Andrenidae
  - Subfamily Andreninae (no records)
  - Subfamily Panurginae
- Family Halictidae
  - Subfamily Rophitinae (no records)
  - Subfamily Nomiinae
  - Subfamily Nomioidinae
  - Subfamily Halictinae
- Family Melittidae
  - Subfamily Dasypodainae
    - Tribe Dasypodaini
    - Tribe Promelittini
    - Tribe Sambini
  - Subfamily Meganomiinae
  - Subfamily Melittinae
- Family Megachilidae
  - Subfamily Fideliinae
  - Subfamily Megachilinae
    - Tribe Lithurgini
    - Tribe Osmiini
    - Tribe Anthidiini
    - Tribe Megachilini
- Family Apidae
  - Subfamily Xylocopinae
    - Tribe Xylocopini
    - Tribe Ceratinini
    - Tribe Allodapini
  - Subfamily Nomadinae
    - Tribe Nomadini
    - Tribe Epeolini
    - Tribe Ammobatini
  - Subfamily Apinae
    - Tribe Eucerini
    - Tribe Anthophorini
    - Tribe Melectini
    - Tribe Meleponini
    - Tribe Apini (records not included)

APPENDIX 2: Map locating places mentioned in the text and captions to figures



INDICES

Index 1: Plant genera and species

A full list of the genera and species of plants from which aculeate wasps and bees were collected as part of the flower visiting survey is available in Gess and Gess (2003)

Index 2: Insect genera and species mentioned in the text

A full list of the genera and species of aculeate wasps and bees collected from flowers as part of the flower visiting survey is available in Gess and Gess (2003)